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Insights about Diversity of Tetrabothriidae (Eucestoda) among Holarctic Alcidae (Charadriiformes): What Is *Tetrabothrius jagerskioeldi*?

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Abstract

Tetrabothriid cestodes are characteristic helminths that infect species of seabirds globally. We begin with the exploration of the diversity of tapeworms of the genus *Tetrabothrius* Rudolphi, 1819 (Eucestoda: Tetrabothriidae), some of which are distributed among seabirds of the family Alcidae (Charadriiformes) at boreal to higher latitudes of Holarctic seas. During the course of 2 decades of field inventory from 1975 through the early 1990s (in addition to earlier collections assembled by Robert L. Rausch and colleagues in Alaska initiated in the late 1940s), an extensive series of tapeworm specimens attributable to species of *Tetrabothrius* was recovered from seabirds across the North Pacific Basin. It was assumed based on published records of species richness in this fauna that a single species, *Tetrabothrius jagerskioeldi* Nybelin, 1916, would predominate among alcid hosts. In contrast, detailed study revealed considerable morphological complexity that could not be accommodated within a single species. Further, it was apparent that the limits for the primary morphological attributes of *T. jagerskioeldi* were not clearly defined. We redescribe *T. jagerskioeldi* based on direct examination of the type series of specimens from Sweden and an assemblage of specimens largely from alcid hosts from the North Pacific basin. Specimens of *T. jagerskioeldi* are diagnosed by a characteristic configuration of the genital atrium, position of the male and female genital canals, structure of the male and female organ systems, and numbers of testes. Based on the spectrum of characters we explored, it was apparent that numerous specimens of *Tetrabothrius* among genera and species of Alcidae from the North Pacific inventory could not be accommodated in *T. jagerskioeldi* and provisionally are referred to *Tetrabothrius* undescribed n. sp. pending ongoing evaluations. Superficially, these are all large and robust tapeworms referable to *Tetrabothrius*, potentially contributing to misidentifications and misattribution that have occurred both in the literature and in the few archived specimens in museums. We summarize the results of extensive inventory collections since 1950, establishing a distributional baseline for species of *Tetrabothrius* from a wide range of geographic localities and an assemblage of host species among the Alcidae and some species of Laridae, Stercorariidae, and Phalacrocoracidae. We further

Supplementary data tables follow the references.

evaluate the validity of historical published records for *T. jagerskioeldi* and other congeners among alcids and other seabirds. A conclusion that emerges is that *T. jagerskioeldi* is a rare tapeworm with a patchy distribution in pelagic to nearshore marine environments, showing considerable heterogeneity in space and time, among alcid seabirds across high-latitude seas of the Holarctic. Prior concepts for host range require reevaluation. We demonstrate that the associations for *T. jagerskioeldi* are relatively narrow and appear to involve a more limited spectrum of alcid hosts, and less often other species of marine birds, than currently assumed. A robust understanding of parasite species diversity and distribution is critical in establishing baselines across marine ecosystems. Our current study among species of *Tetrabothrius*, especially in the North Pacific basin and Bering Sea ecosystem contributes to development of a series of specimen-centered baselines derived primarily from the late 1970s to the early 1980s against which accelerating perturbations linked to climate warming and ocean-atmosphere interactions may be explored. Detailed knowledge of specimen-based faunal diversity for parasites provides a cumulative, temporal, and spatial snapshot and proxy for conditions in marine foodwebs and the continuity of trophic linkages.

Keywords: *Tetrabothrius jagerskioeldi*, Alcidae, macroparasites, marine diversity, specimen archives, comparative morphological, host, geographical baselines

Introduction

Helminth parasites of seabirds hold substantial information about the status and sustainability of marine ecosystems (Hoberg, 1996; Muzaffar, 2009). Species diversity, host range and geographic distribution are driven by climatological, oceanographic, and anthropogenic factors that influence the structure of trophic linkages on which parasite life cycles and transmission dynamics are dependent (Galaktionov, 1995; Hoberg, 1996; 2005). Consequently, parasites serve as direct indicators and as proxies for conditions in marine foodwebs over evolutionary and ecological time (e.g., Hoberg and Brooks, 2008; Hoberg et al., 2013). Parasite distributions demonstrate the outcomes of often subtle oscillations in atmospheric and sea-surface temperature, including regime shifts such as those of the El Niño Southern Oscillation and the Pacific Decadal Oscillation that initiate cascades in marine foodwebs on varying spatial and temporal scales (Mouritsen and Poulin, 2002; Chavez et al., 2003; Hurrell et al., 2003; Sydeman et al., 2015; Hoberg et al., 2017).

Insights about the diversity of parasites in marine birds (and other vertebrates) depend on the development of robust information on expansive spatial and temporal scales. Baselines for biodiversity information, transcending populations to species and ecosystems, emerge from field collections and archival deposition of specimens in permanent museum repositories (e.g., Cook et al., 2013, 2017; Hoberg et al., 2013; Brooks et al., 2014; Dunnum et al., 2017). Specimens in synergy with their associated data constitute the fabric of biodiversity informatics, becoming the gateway to explore dynamic change in the biosphere. Archives of specimens and information are the cornerstones to reveal ecological connectivity and perturbation emerging from the acceleration of climate forcing, other anthropogenic factors, and natural events. Parasite faunal baselines will contribute to identifying and understanding the scope of ecological perturbation, including shifting production cycles, trophic dynamics, and mortality events emerging across the Bering Sea ecosystem and broader North Pacific basin (e.g., Jones et al., 2019).

At the core of biodiversity informatics is the accurate identification of species. In the current paper we begin the exploration of the diversity of tapeworms of the genus *Tetrabothrius* Rudolphi, 1819 (Eucestoda: Tetrabothriidae), some of which are distributed among seabirds of the family Alcidae (Charadriiformes) at boreal to higher latitudes of Holarctic seas. The Alcidae is a small avian group including 24 extant species with an extended history during the late Tertiary in marine environments of the Northern Hemisphere (e.g., Moum et al., 1994; Friesen et al., 1996; Smith, 2011). Conventional wisdom for tetrabothriids is that a single species, *Tetrabothrius jagerskioeldi* Nybelin, 1916, among 52 recognized congeners (Mariaux et al., 2017), is geographically widespread across polar and boreal seas and occurs within a considerable number of the 24 extant species of alcids representing multiple avian tribes (e.g., Baer, 1954; Temirova and Skrjabin, 1978; Hoberg, 1984; Muzaffar and Jones, 2004). Baer (1954) proposed synonymy

for *Tetrabothrius intrepidus* Baylis, 1919 with *T. jagerskioeldi*, reinforcing the concept for a broad geographic and host distribution.

During the course of 2 decades of field inventory from 1975 through the early 1990s (in addition to earlier collections assembled by Robert L. Rausch and colleagues in Alaska initiated in the late 1940s), an extensive collection of tapeworms attributable to species of *Tetrabothrius* was recovered from seabirds across the greater North Pacific Basin (e.g., Hoberg, 1984; Table 1; Supplementary Data Table 1; Supplementary Data Table 2). During the 1990s, focused investigations of diversity in this assemblage of specimens, primarily in seabirds of the families Alcidae and Laridae, were initiated but not brought to completion. It was assumed at that time, based on published records of species richness in this fauna, that a single species, *Tetrabothrius jagerskioeldi*, would predominate among alcid hosts.

In contrast, detailed study revealed considerable morphological complexity that could not be accommodated within a single species. Further, the limits for the primary morphological attributes of *T. jagerskioeldi* were not clearly defined. Characterization of morphology tended to be incomplete or ambiguous, and this was a common theme in the original description by Nybelin (1916) and in subsequent examinations and redescriptions of tapeworms attributed to this species from localities primarily in the North Atlantic Basin and Arctic Ocean (e.g., Baer, 1954; Temirova and Skrjabin, 1978). Some descriptions were repeated across multiple publications (e.g., Temirova and Skrjabin, 1978; Ryzhikov et al., 1985). Further, published reports of species occurrence across high latitude seas were generally not accompanied by specimens and comparative morphological evaluations (e.g., Belopol'skaia, 1952, 1963a, 1963b; Baer, 1956; Threlfall, 1971; Smetanina 1979, 1981; Smetanina and Leonov, 1984). Despite records of *T. jagerskioeldi* in a relatively broad literature which established an apparent Holarctic range, specimens of this and other species of *Tetrabothrius* were rarely archived, even from very extensive inventories, as vouchers in museum repositories (e.g., Threlfall, 1971; Muzaffar and Jones, 2004; Muzaffar, 2009). Consequently, the potential was limited for comparative studies linking taxonomy and identification with the spatial and temporal aspects of distribution. An essential question requiring resolution, and as a requisite gateway to definitions of diversity within this fauna, was the following: What is *T. jagerskioeldi*, its host range, and geographic distribution?

As the foundation to resolve the identity of *T. jagerskioeldi*, and thus to provide a pathway for defining morphologically based species limits within an apparent complex of cryptic species, the original type specimens held in the Naturhistoriska Museet, Göteborg, Sweden, were examined. Other specimens attributed to *T. jagerskioeldi* in the collections of the Museum d'Histoire Naturelle, Geneva, Switzerland, were evaluated. Additionally, the type series of *T. intrepidus* Baylis, 1919, an apparent synonym of *T. jagerskioeldi*, held at the British Museum of Natural History was studied. Other specimens of *Tetrabothrius* in alcid hosts, but which were unattributed to species, were also examined from the Museum National d'Histoire Naturelle, Paris. New data derived from these specimens is presented in the context of standardized approaches recognizing progressive ontogenetic changes in the strobila, proglottids, and organ systems to define structural diversity in the Tetrabothriidae (e.g., Murav'eva and Popov, 1976; Hoberg, 1987; Hoberg et al., 1991). The identity of *T. jagerskioeldi* is now firmly established and is explored in our current study. Relative to field inventory across the North Pacific, the occurrence of *T. jagerskioeldi* was confirmed, whereas multiple previously unrecognized cryptic species partitioned among the alcids were revealed (Supplementary Data Table 2).

Our current study focuses on a complete redescription and definition for *T. jagerskioeldi* as a comparative morphological baseline. We report the first specimens and observations of *T. jagerskioeldi* confirmed in host species and localities from the North Pacific Basin, Bering Sea, and Sea of Okhotsk. New hosts and geographic records are documented by archival specimens from the region of the North Pacific Basin. Further, we summarize the results of extensive inventory collections since 1950 establishing a distributional baseline for species of *Tetrabothrius* from a wide range of geographic localities and an assemblage of host species among the Alcidae and some species of Laridae, Stercorariidae, and Phalacrocoracidae (Table 1; Supplementary Data Table 1; Supplementary Data Table 2). We further evaluate the validity of historical published records for *T. jagerskioeldi* and other congeners among alcids and other seabirds. In providing a firm foundation for *T. jagerskioeldi*, we establish the basis for a series of taxonomic decisions and descriptions to characterize previously unrecognized diversity among species of *Tetrabothrius*, primarily associated with alcid host species, that will build and follow on our current study.

Table 1. Avian Specimens (Alcidae, Laridae, Stercorariidae, and Phalacrocoracidae) from the Greater North Pacific Basin Examined for Helminth Parasites (1949–1992)

Species	Number
Charadriiformes—Alcidae	
Tribe Alcini	
Alle alle (Linnaeus) (dovekie)	1
Uria aalge (Pontoppidan) (common murre)	275
Uria lomvia (Linnaeus) (thick-billed murre)	150
Tribe Cepphini	
Cepphus carbo Pallas (spectacled guillemot)	4
Cepphus columba Pallas (pigeon guillemot)	22
Cepphus grylle (Linnaeus) (black guillemot)	8
Tribe Brachyramphini	
Brachyramphus marmoratus (Gmelin) (marbled murrelet)	7
Brachyramphus brevirostris (Vigors) (Kittlitz's murrelet)	3
Tribe Synthliboramphini	
Synthliboramphus antiquus (Gmelin) (ancient murrelet)	50
Synthliboramphus scrippsi (Green and Arnold) (Scripp's murrelet)	4
Tribe Aethiini	
Ptychoramphus aleuticus Brandt (Cassin's auklet)	16
Aethia psittacula (Pallas) (parakeet auklet)	56
Aethia cristatella (Pallas) (crested auklet)	190
Aethia pygmaea (Gmelin) (whiskered auklet)	18
Aethia pusilla (Pallas) (least auklet)	62
Tribe Fraterculini	
Cerorhinca monocerata (Pallas) (rhinoceros auklet)	39
Fratercula cirrhata (Pallas) (tufted puffin)	285
Fratercula corniculata (Naumann) (horned puffin)	144

Species	Number
Charadriiformes—Laridae	
Rissa tridactyla (Linnaeus) (black-legged kittiwake)	206
Rissa brevirostris (Bruch) (red-legged kittiwake)	2
Larus hyperboreous Gunnerus (glaucous gull)	13
Larus glaucescens (Naumann) (glaucous-winged gull)	65
Larus schistisagus Stejneger (slaty-backed gull)	27
Larus argentatus (Pontoppidan) (herring gull)	12
Larus heermani Cassin (Heerman's gull)	6
Sterna paradisaea Pontoppidan (Arctic tern)	37
Onychoprion aleutica (Baird) (Aleutian tern)	1
Xema sabini (Sabine) (Sabine's gull)	34
Charadriiformes—Stercorariidae	
Stercorarius pomarinus Temminck (pomarine jaeger)	14
Stercorarius parasiticus (Linnaeus) (parasitic jaeger)	4
Stercorarius longicaudus Vieillot (long-tailed jaeger)	18
Suliformes—Phalacrocoracidae	
Urile pelagicus (Pallas) (pelagic shag)	23
Urile "kenyoni" (Siegel-Causey) (Kenyon's shag) = *U. pelagicus*	2
Urile urile (Gmelin) (red-faced shag)	28
Specimens Examined	**1,826**
Species Examined	**34**

Methods and Materials

Correct Nomenclature

These large cestodes, primarily among the Alcidae, are often shown under the spelling of *T. jagerskioldi* or *T. jagerskiöldi*, which is most prevalent in common usage (e.g., Yamaguti, 1959; Schmidt, 1986; Temirova and Skrjabin, 1978; Muzaffar and Jones, 2004). This nomenclature is incorrect according to Article 32 of the 4th Edition of the International Code of Zoological Nomenclature (ICZN, 1999). Nybelin (1916) presented the original spelling as *Tetrabothrius jägerskiöldi*, the species name accepted by Fuhrmann (1932), Joyeux and Baer (1936), and Baer (1954, 1956). The correct spelling, as shown by Ryzhikov et al. (1985) and Mariaux et al. (2017), and accepted in the current manuscript, is *Tetrabothrius jagerskioeldi*.

Primary Collection Localities North Pacific Basin

Alaska: Aleutian Islands region, Bering Sea region, Arctic Basin and Chukchi Sea, Gulf of Alaska region; Eastern North Pacific: California and Washington State; Russian Subarctic and Arctic: Northern Sea of Okhotsk, East Siberian Sea, and Chaun Gulf. Host species and specimens examined are summarized in Table 1 and include 18 species of Alcidae, 10 Laridae, 3 Stercorariidae, and 3 Phalacrocoracidae. Complete localities, dates, and collectors for field-based biodiversity inventory are outlined in Supplementary Data Table 1. Specimens confirmed and attributed to *T. jagerskioeldi* from these localities and hosts have been archived in the Parasite Division of the Museum of Southwestern Biology, University of New Mexico, as specified in Supplementary Data Table 2 and Supplementary Data Table 3.

Additionally, for discussion in the text the geographic coordinates and place names for localities of seabird colonies and Nature Reserves (Zapovednika) originally reported in the Russian literature are amended for clarity. (1) The Sudzukhinsky Zapovednik is a former name of the Lazovsky Zapovednik, which is located in the south of Primorskiy Krai, Russian Far East (43°14′0″N, 133°24′0″E) and is the site of collections reported by Belopol'skaia (1963a, 1963b). (2) Peter the Great Bay, Russian Far East, adjacent to Vladivostok (42°40′N, 132°00′E) is the site of collections reported by Smetanina (1979, 1981). (3) Kharlov Island Barents Sea, Russia (68°48′25″N, 37°20′37″E) is the largest island of the Seven Islands Archipelago and site of collections summarized by Galkin et al. (2005). Seven Islands is adjacent to the Kola (Kolskiy) Peninsula coast, Barents Sea (the coast of the Kola Peninsula to the east of the Kola Fjord is called East Murman), and the site of the largest seabird colonies in this region. (4) The Seven Islands State Natural Reserve (Sem' Ostrov Gosudarstvennogo Zapovednik) was the site of collections reported by Belopol'skaia (1952) based on field work in the early 1940s. In the 1960s the Seven Islands State Natural Reserve was incorporated into the Kandalaksha State Natural Reserve (Kandalakshskiy Gosudarstvennogo Zapovednik). (5) Bezymiannaya Bay, Novaya Zemlya, Russian Arctic (72°54′N, 53°10′E) is the site of collections reported by Markov (1941). (5) Hooker Island, is in the archipelago defined by Franz Josef Land in the high Arctic (80°18′N, 53°21′E) and is the site of collections reported by Galkin et al. (2005).

Specimens Examined

Tetrabothrius jagerskioeldi Nybelin, 1916

Type series – consisting of 5 slides held in the Naturhistoriska Museet, Göteborg, Sweden, in a series prepared and described by Orvar Nybelin in 1916 based on specimens collected by L. A. Jägerskiöld in a black guillemot, *Cepphus grylle* (Linnaeus), at Bohuslän, Kristineberg, Sweden (ca. 58°14′N, 11°22′E), on 28 July 1910 (Nybelin, 1916). These included 3 slides marked "type" respectively—a whole mount with 5 segments, transverse sections from mature, and transverse sections from gravid; 2 additional slides not marked "type" but from the same host and locality included frontal sections of mature proglottids and transverse sections of early mature proglottids. *Voucher series* – Additionally an early mature specimen was collected by O. Nybelin on 18 July 1916 in *C. grylle* at Bohuslän, Väderöarna (Weather Islands Archipelago), Sweden (ca. 58°34′N, 11°03′E) (labeled No. 1916-2915) but was held in ethanol and not mounted or included in the original description. In February 1995 this specimen was processed for examination. In total 4 slides were prepared, with strobila or sections stained in Semichon's acetic carmine, and mounted in Canada balsam: (1) 25 proglottids were cut from the terminal end of the cestode for preparation of hand-cut, transverse thick sections; (2) anterior of the remaining strobila with scolex was mounted dorsally; (3) 5 proglottids were mounted ventrally; (4) 6 mature proglottids were mounted dorsally, with the tegument removed to facilitate viewing of internal anatomy.

Other Material: (1) 2 specimens on 1 slide attributed to this species held in the Museum d'Histoire Naturelle, Geneva (No. 108/60), collected by J. G. Baer on 27 July 1955 from near Kangerluk (formerly Diskofjord), West Greenland (ca. 69°29′N, 53°56′W) in *Cepphus grylle* are determined to represent an undescribed species (E. P. Hoberg, unpublished data). (2) 1 specimen on 3 slides attributed to this species held in the Museum d'Histoire Naturelle, Geneva (No. 108/61-63), collected by J. G. Baer on 6 August 1955 from Oqaitsoq (near Disko Island), West Greenland (ca. 69°55′N, 51°22′W) in a razorbill, *Alca torda* Linnaeus, is redetermined as *T. erostris* (Lönnberg, 1896) in the current study (E. P. Hoberg, unpublished data).

Tetrabothrius intrepidus Baylis, 1919 [Confirmed as junior synonym of *T. jagerskioeldi* consistent with Baer, 1954]

Type series – consisting of 4 slides held in the British Museum of Natural History (1919.6.14.24) collected by E. A. Cockayne on 27 June 1917 in *Cepphus grylle* from "Yukanski," Kola Peninsula, Russia (apparently in the Yukanski Islands, adjacent to Ostrovny, Russia, ca. 68°3′N, 39°30′E), and described by H. A. Baylis (1919). Subsequently, 4 slides were prepared in November 1995 from ethanol-preserved specimens in the type series, including hand-cut thick sections to study the genital atrium.

Other Material: (1) A specimen attributed to *T. intrepidus* held in the Museum d'Histoire Naturelle, Geneva (No. 65/72-73), from Reykjavik, Iceland (ca. 64°09′N, 21°57′W), in *Cepphus grylle* appears consistent with the original description. (2) Additional specimens held in the British Museum and attributed to *T. intrepidus* in *Uria aalge* (Pontoppidan) under 1976.4.21.80 collected by G. Rees adjacent to Cardiganshire, Wales, United Kingdom (ca. 51°35′N, 3°45′W) and 1984.10.15.1-6 collected by J. Vercruysse, presumably in the North Sea adjacent to the

Netherlands, are referable to *Tetrabothrius erostris* (E. P. Hoberg, unpublished data). (3) Unattributed specimens in *Uria aalge* [reported as *Uria troile* (Linnaeus)] from the coastal region of Concarneau, France (ca. 47°51′N, 3°55′W), held in the Museum National d'Histoire Naturelle, Paris, were also examined, with new slides prepared; these specimens were also consistent with *T. erostris* (E. P. Hoberg, unpublished data).

North Pacific Basin/Sea of Okhotsk Vouchers – E. P. Hoberg, R. L. Rausch, and colleagues

Specimens of *Tetrabothrius* were examined based on field collections of 1,826 avian specimens representing 34 species across 43 geographic localities in the North Pacific Basin and East Siberian Sea. Complete data for hosts, localities, and dates of collection are summarized (Table 1; Supplementary Data Tables 1 and 2). Complete specimen data and identification of *T. jagerskioeldi* and other species are documented, along with data for deposition in the Division of Parasitology and collections of the Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM (Supplementary Data Table 3) (http://arctos.database.museum). Identifications and species attributions for this series of specimens were limited to comparative morphological approaches. Molecular phylogenetic analyses were not possible for specimens because of their age and time frames for field collections in the 1950s to late 1980s, and a long history of storage at ambient temperatures in 10% formalin, varying grades of ethanol, and other reagents.

Results

Identity of T. jagerskioeldi *in Historical Collections*

Excluding the type series for *T. jagerskioeldi* and *T. intrepidus*, few specimens were available in museum repositories representing North America and Eurasian collections (Table 2; Table 3). The identity and disposition of these specimens has been outlined under the section above exploring specimens examined during our study. Among these, a single specimen of *T. jagerskioeldi* (attributed to *T. intrepidus*) was confirmed in *C. grylle* from Reykjavik, Iceland. A series of 6 specimens from 5 localities were misidentified (referred to incorrect species) or misattributed (not recognized as undescribed). These include 3 specimens in *U. aalge* from western Europe and a single specimen in *Alca torda* from West Greenland, all attributable to *T. erostris*. Additionally, 2 specimens in *C. grylle* from West Greenland are consistent with a currently undescribed species of *Tetrabothrius*. The majority of reports in the literature were not accompanied by deposition of voucher specimens.

Distribution of Tetrabothrius *spp. in the North Pacific Inventory*

Specimens of *Tetrabothrius* were examined based on field collections of 1,826 marine birds of 34 species from 7 regions and 43 localities across the greater North Pacific Basin (Table 1, Supplementary Data Table 1, Supplementary Data Table 2). Collections included 1,334 alcids of 18 species, 403 larids (10 species), 36 stercorariids (3 species), and 53 phalacrocoracids (3 species). Overall species of *Tetrabothrius* were distributed in 349 hosts (not accounting for multispecies infections) among 1,826 seabirds examined (prevalence = 19%). We confirmed the identity of *T. jagerskioeldi* in alcid (6 species), larid (1), and phalacrocoracid (1) hosts based on these collections and direct comparisons to the type series of Nybelin (1916) (Table 2; Supplementary Data Table 2; Supplementary Data Table 3).

Specimens of *T. jagerskioeldi* occurred in 29 of 1,826 birds (overall, 1.5% prevalence). Infections were observed primarily among alcid hosts, including 6 of 18 species examined at 7 of 43 localities and among 14 of 1,334 avian specimens (1% prevalence; range in intensity = 1–9 per host) (Table 3; Supplementary Data Table 2). Infections of *T. jagerskioeldi* were most often observed among guillemots, including *C. columba* (22 examined, 8 infected, 37% prevalence), *C. grylle* (8 examined, 1, 12.5%), and *C. carbo* (4 examined, 2, 50%). Other alcids were rarely observed as hosts, with cestodes occurring in single specimens of *U. aalge* at Shuyak Island (275 examined, 1, < 1%), *B. marmoratus* at Kodiak Island (7 examined, 1, 14.5%), and *C. monocerata* in pelagic environments south of the Aleutian Islands (39 examined, 1, 2.5%).

Among non-alcid hosts, *T. jagerskioeldi* occurred in 15 of 492 avian specimens examined (3% prevalence) at 3 of 43 localities; it was not observed in stercorariids. Among larids, 14 of 403 specimens (3.5% prevalence; range in intensity= 1–4) in 1 of 10 species were hosts across 2 of 43 localities, with *T. jagerskioeldi* observed in *Larus glaucescens* (Naumann) from the northern Gulf of Alaska. Among glaucous-winged gulls,10 of 20 (prevalence = 50%) were hosts at Puffin Island, and 4 of 20 (20%) at Central Island. Among phalacrocoracids, 1 of 53 specimens (1.9%) among 3 species was a host at a single locality, with a single specimen of *T. jagerskioeldi* observed in *Urile pelagicus* (Pallas) at Buldir Island from the far western Aleutian Islands.

Table 2. Morphological Data, Hosts, and Geographic Localities for *Tetrabothrius jagerskioeldi* Nybelin, 1916 from Published Sources and the North Pacific Inventory

Character	*T. jagerskioeldi*[1]	*T. intrepidus*[2]	*T. jagerskioeldi*[3]	*T. jagerskioeldi*[4]	*T. jagerskioeldi*[5]	*T. jagerskioeldi*[6]	*T. jagerskioeldi*[7]
Host(s) Species	*Cepphus grylle*	*Cepphus grylle*	*Alca torda*, *Cepphus grylle*, *Uria aalge* (*Uria troile*)	*Alca torda*, *Cepphus grylle*, *Cepphus carbo*, *Fratercula arctica*, *Fratercula cirrhata*, *Stercorarius parasiticus*, *Synthliboramphus antiquus*, *Uria aalge* (*Uria troile*)	*Alca torda*, *Cepphus grylle*, *Cepphus carbo*, *Fratercula arctica*, *Fratercula cirrhata*, *Stercorarius parasiticus*, *Synthliboramphus antiquus*, *Uria aalge* (*Uria troile*)	*Brachyramphus marmoratus*, *Cepphus grylle*, *Cepphus carbo*, *Cepphus columba*, *Cerorhinca monocerata*, *Uria aalge*	*Larus glaucescens*, *Urile pelagicus*
Geographic Locality	Kristineberg, Sweden; Väderöarna, Sweden (*)	Yukanski, Russia; Reykjavik, Iceland (*)	North Atlantic Basin; Barents Sea	Europe (Sweden, Greenland, North Atlantic, Barents Sea); Chukotka, Kurile Islands	Greenland; Sweden; Russia (Barents Sea, Chukotka, Kurile islands)	North Pacific Basin (Gulf of Alaska, Bering Sea, Aleutian Islands); Sea of Okhotsk	North Pacific Basin (Gulf of Alaska, Aleutian Islands)
Strobila (L × W mm, maximum)	90 × 4	___ × 3	60–90 × 4	40–90 × 3.5–4.5	40–90 × 3.5–4.5	85–203 × 3.9	101–158 × 4.5
Muscle Bundles, outer (#)	202–221 (*)	~100	not specified	121	121	185–237	143–184
Fibers/bundle outer (#)	3–12 (*)	not counted (*)	not specified	12	12	3–11	not counted
Muscle Bundles, inner (#)	118–125 (*)	not counted (*)	not specified	81	81	99–146	60–104
Fibers/bundle, inner (#)	5–53 (*)	not counted (*)	not specified	19–22	19–22	6–37	not counted
Scolex (L)	510 (original); 325 (*)	461–550 (*)	520	520–620	520–620	350–580	393–632
Scolex (W)	560 (original); 430 (*)	600 (original); 597–650 (*)	617	290–570	290–570	490–700	477–786
Bothridia (L)	285–300 (*)	371–500 (*)	not specified	not specified	not specified	240–500	not measured
Bothridia (W)	195–215 (*)	310–335 (*)	not specified	not specified	not specified	235–370	not measured
Neck (L)	short (*)	short (*)	not specified	short	absent	short	short
Genital Pore (position)	dextral (*)	dextral (*)	not specified	dextral	dextral	dextral	dextral
Genital Ducts (relation to osmoregulatory canals)	between (*)	between (*)	not specified	ventral[8]	not specified	between	between
Cirrus Pouch (diameter)	100–111 (original); 70–114 (*) (mature to gravid)	96–130 (*)) (pregravid	91–114	80–94	80–94	65–110 (mature); 75–152 (pregravid to gravid)	60–119 (mature); 88–132 (pregravid to gravid)
Genital Atrium (diameter)	117–169 (*) (mature to gravid)	143–169 (*) (pregravid to gravid)	not specified	240 × 150–160	240 × 150–160	125–190 (mature); 112–230 (pregravid to gravid)	95–203 (mature); 145–238 (pregravid to gravid)
Structure Male Papilla	triangular (*)	triangular (*)	not specified	not specified	not specified	triangular	triangular
Genital Ducts (position in genital atrium)	opens center of papilla (male); female at base, ventral (*)	opens center of papilla (male); female at base, ventral (*)	opens center of papilla (male); female at base, ventral (*)	opens center of papilla (male); female at base, ventral (*)	not specified	opens center of papilla (male); female at base, ventral (*)	opens center of papilla (male); female at base, ventral (*)
Male Canal (L)	39–57 (*) (mature); 44–49 (*) (gravid)	44–55 (*) (pregravid)	45	not specified	not specified	41–50 (mature); 37–62 (late mature to pregravid)	34–65 (mature to pregravid)

Table 2. Morphological Data, Hosts, and Geographic Localities for *Tetrabothrius jagerskioeldi* Nybelin, 1916 from Published Sources and the North Pacific Inventory *(continued)*

Character	*T. jagerskioeldi*[1]	*T. intrepidus*[2]	*T. jagerskioeldi*[3]	*T. jagerskioeldi*[4]	*T. jagerskioeldi*[5]	*T. jagerskioeldi*[6]	*T. jagerskioeldi*[7]
Testes (#)	58–62 (original); 46–58 (*)	50	48–58	48–56	48–58	40–70	40–73
Ovary (W)	410–600 (mature) (*)	not measured (*)	not specified	940–1,020	940–1,020	420–980 (maximum)	560–1,335 (maximum)
Vitelline Gland (W × L)	101–192 × 44–120 (*) (mature)	182–208 (W) (*) (pregravid)	not specified	340 × 160	340 × 160	120–400 × 48–170 (mature to pregravid)	107–345 × 52–155 (mature); 179–370 (W) (pregravid)
Vitelline Gland (structure)	globular (*)	globular (*)	globular	globular	globular	globular	globular
Vitelline Duct	single (*)	single (*)	not specified	not specified	not specified	single	single
Vaginal Seminal Receptacle	spindle-shaped, level of osmoregulatory canals (*)	spindle-shaped, level of osmoregulatory canals (*)	not specified	spindle-shaped, level of osmoregulatory canals	not specified	spindle-shaped, level of osmoregulatory canals	spindle-shaped, level of osmoregulatory canals
Uterus position (relative to osmoregulatory canals)	between (*)	between (*)	not specified	not specified	not specified	between	between
Embryophore (L × W)	not observed	22–37 × 30–41 (*)	not specified	not specified	not specified	28–35 × 34–43	not measured
Oncosphere (L × W)	not observed	18–23 × 25–33 (*)	not specified	21 × 34	not specified	20–26 × 28–39	21–31 × 29–44

Notes:

All measurements are in micrometers (µm) unless otherwise indicated.

1. Nybelin (1916) from original description; asterisk (*) indicates new observations from type and voucher specimens in current study.
2. Baylis (1919) from original description; asterisk (*) indicates new observations from type specimens in current study; considered a synonym of *T. jagerskioeldi*.
3. Baer (1954). Redescription likely based on type specimens of Nybelin (1916). Includes list of prior records of known host species. Host species are unconfirmed based on voucher specimens.
4. Temirova and Skriabin (1978). Description in part from single specimens in *Cepphus carbo*, *Fratercula arctica*, and *Stercorarius parasiticus*. Includes list of known and unconfirmed host species and geographic localities from prior records; without voucher specimens.
5. Ryzhikov et al. (1985) repeats Temirova and Skriabin (1978). Includes list of known and unconfirmed host species and geographic localities; without voucher specimens.
6. Current study North Pacific; specimens in Alcidae hosts. Confirmed based on direct comparisons to type specimens.
7. Current study North Pacific; specimens in Laridae and Phalacrocoracidae hosts. Confirmed based on direct comparisons to type specimens.
8. Based on apparent position depicted in figures but not specifically stated in text.

Table 3. Substantiated and Unsubstantiated Records of Host and Geographic Occurrence for *Tetrabothrius jagerskioeldi* Nybelin, 1916 and *T. jagerskioeldi* Complex among Alcidae and Other Seabirds

Host Taxonomy	Avian Species	*Tetrabothrius jagerskioeldi*	*Tetrabothrius* undescribed n. sp.
Alcidae			
Tribe Alcini	*Alca torda* Linnaeus, 1758	Seven Islands Reserve, Barents Sea (Belopol'skaia, 1952) ▲	cannot be determined: no specimens are available
	Alle alle (Linnaeus, 1758)	Northwestern North Atlantic (Threlfall, 1971) ?▲	cannot be determined: no specimens are available
	Uria aalge (Pontoppidan, 1763)	Seven Islands Reserve, Barents Sea (Belopol'skaia, 1952) ▲ Northwestern Atlantic (Threlfall, 1971) ▲ Big Bay, Shuyak Island, Gulf of Alaska ❋★	Chiniak Bay, Kodiak Island, Gulf of Alaska ❋ St. Matthew Island, Bering Sea ❋ Cape Lisburne, Chukchi Sea ❋ Talan Island, Sea of Okhotsk ❋ Grays Marine Canyon, Eastern North Pacific ❋ Humboldt Bay, Eastern North Pacific ❋
	Uria lomvia (Linnaeus, 1758)	Northwestern Atlantic (Threlfall, 1971) ▲ Peter the Great Bay, Russian Far East (Semtanina, 1979, 1981) ▲	Ugaiushak Island, Gulf of Alaska ❋ Buldir Island, Western Aleutian Islands ❋ Western Aleutian Islands (pelagic) ❋ St. Lawrence Island, Bering Sea ❋ St. Matthew Island, Bering Sea ❋ Cape Thompson, Chukchi Sea ❋ Talan Island, Sea of Okhotsk ❋
	†*Pinguinus impennis* (Linnaeus, 1758)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	Host specimen(s) examined: *T. jagerskioeldi* complex not discovered
Tribe Cepphini	*Cepphus carbo* Pallas, 1811	Sudzukhinsky Reserve, Russian Far East (Belopol'skaia, 1963a, 1963b) ▲ Peter the Great Bay, Russian Far East (Smetanina, 1979, 1981) ▲ Northern Sea of Okhotsk ❋★	no current specimens or records
	Cepphus columba Pallas, 1811	St. Lawrence Island, Bering Sea ❋✪★ Uganik Bay, Kodiak Island, Gulf of Alaska ❋✪★ Uyak Bay, Kodiak Island, Gulf of Alaska ❋✪★ St. Matthew Island, Bering Sea ❋✪★ Sledge Island, Bering Sea ❋✪★ Ugaiushak Island, Gulf of Alaska ❋ ✪★	St. Lawrence Island, Bering Sea ❋ St. Matthew Island, Bering Sea ❋
	Cepphus grylle (Linnaeus, 1758)	Kristineberg, Sweden (Nybelin, 1916) ❋ Väderöarna, Sweden ❋ Barents Sea (Baylis, 1918) ❋ Seven Islands Reserve, Barents Sea (Belopol'skaia, 1952) ▲ Seven Islands Reserve, Barents Sea (Kuklin and Kuklina, 2005) ▲ Reykjavik, Iceland ❋★ Boxer Bay, St. Lawrence Island, Bering Sea ❋★	Kangerluk, West Greenland (Baer, 1956) ❋

Table 3. Substantiated and Unsubstantiated Records of Host and Geographic Occurrence for *Tetrabothrius jagerskioeldi* Nybelin, 1916 and *T. jagerskioeldi* Complex among Alcidae and Other Seabirds *(continued)*

Host Taxonomy	Avian Species	*Tetrabothrius jagerskioeldi*	*Tetrabothrius* undescribed n. sp.
Tribe Brachyramphini	*Brachyramphus marmoratus* (Gmelin, 1789)	Chiniak Bay, Kodiak Island, Gulf of Alaska ❋✪★	no current specimens or records
	Brachyramphus brevirostris (Vigors, 1829)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	no current specimens or records
	Brachyramphus perdix ⊙ (Pallas, 1811)		
Tribe Synthliboramphini	*Synthliboramphus antiquus* (Gmelin, 1789)	Sudzukhinsky Reserve, Russian Far East (Belopol'skaia, 1963a, 1963b) ▲ Peter the Great Bay, Russian Far East (Smetanina, 1979, 1981) ▲	Western Aleutian Islands (pelagic) ❋ St. Lawrence Island, Bering Sea ❋
	Synthliboramphus craveri ⊙ (Salvadori, 1865)		
	Synthlibramphus hypoleucus ⊙ (Xantus de Vesey, 1860)		
	Synthliboramphus scrippsi (Green and Arnold, 1939)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	Santa Barbara Island, Channel Islands, Eastern North Pacific ❋
	Synthliboramphus wumizuzume ⊙ Temminck, 1836		
Tribe Aethiini	*Ptychoramphus aleuticus* (Pallas, 1811)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	Grays Marine Canyon, Eastern North Pacific ❋
	Aethia psittacula (Pallas, 1769)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	Talan Island, Sea of Okhotsk ❋
	Aethia cristatella (Pallas, 1769)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	Amchitka Island, Central Aleutian Islands ❋ St. Paul Island, Bering Sea ❋ Talan Island, Sea of Okhotsk ❋
	Aethia pygmaea (Gmelin, 1789)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	Buldir Island, Western Aleutian Islands ❋
	Aethia pusilla (Pallas, 1811)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	St. Matthew Island, Bering Sea ❋

Table 3. Substantiated and Unsubstantiated Records of Host and Geographic Occurrence for *Tetrabothrius jagerskioeldi* Nybelin, 1916 and *T. jagerskioeldi* Complex among Alcidae and Other Seabirds *(continued)*

Host Taxonomy	Avian Species	*Tetrabothrius jagerskioeldi*	*Tetrabothrius* undescribed n. sp.
Tribe Fraterculini	*Fratercula arctica* (Linnaeus, 1758)	Seven Islands Reserve, Barents Sea (Belopol'skaia, 1952) ▲ Northwestern Atlantic (Threlfall, 1971) ▲	cannot be determined; no specimens are available
	Fratercula cirrhata (Pallas, 1769)	Russian Far East or Kurile Islands (?) (Temirova and Skrjabin, 1978) ▲	Western Aleutian Islands (pelagic) ❋ Talan Island, Sea of Okhotsk ❋
	Fratercula corniculata (Naumann, 1821)	Host specimen(s) examined: *T. jagerskioeldi* not discovered	Ugaiushak Island, Gulf of Alaska ❋ Chiniak Bay, Kodiak Island, Gulf of Alaska ❋ Buldir Island, Western Aleutian Islands ❋ Western Aleutian Islands (pelagic) ❋ Talan Island, Sea of Okhotsk ❋
	Cerorhinca monocerata (Pallas, 1811)	Shikotan Island, Kurile Islands (Smetanina and Leonov, 1984) ▲ Western Aleutian Islands (pelagic) ❋★	Grays Marine Canyon, Eastern North Pacific ❋ Destruction Island, Straits of Juan de Fuca, Eastern North Pacific ❋
Laridae	*Larus glaucescens* Naumann, 1840	Central Island, Gulf of Alaska ❋✪★ Puffin Island, Gulf of Alaska ❋✪★	no current specimens or records
Stercorariidae	*Stercorarius parasiticus* (Linnaeus, 1758)	Seven Islands Reserve, Barents Sea (Belopol'skaia, 1952) ▲	cannot be determined; no specimens are available
Phalacrocoracidae	*Urile pelagicus* (Pallas, 1811)	Buldir Island, Western Aleutian Islands ❋✪★	no current specimens or records

Notes:

⊙ Species of Alcidae lacking parasitological data and which apparently have not been examined for parasites.

▲ Historical record not supported by archival specimens.

❋ Record substantiated by permanent archived specimens held in an international museum collection; specimens examined during the current study.

✪ New host record.

★ New geographic record.

Field inventory from the North Pacific basin also revealed a putative complex of cryptic, undescribed species limited in distribution to alcid hosts. Collectively these are large strobilate tetrabothriids which share considerable superficial similarity to specimens of *T. jagerskioeldi*. These specimens, designated here as *Tetrabothrius* n. sp.–undescribed, represent a minimum of 4 previously unrecognized species-level taxa. Specimens of the putative complex occurred in 102 of 1,334 birds examined (8% prevalence) among 13 of 18 species of North Pacific Alcidae (range in intensity = 1–19) from 15 of 43 localities (Table 3; Supplementary Data Table 2); prevalence across all 1,826 specimens of seabirds sampled = 6%. These putative cryptic species were not observed in other species of seabirds (larids, stercorariids, or phalacrocoracids) across the scope of collections in the North Pacific basin. Comparative morphological characterization and evaluation of this apparent cryptic assemblage as the basis for taxonomic decisions is deferred to subsequent studies among *Tetrabothrius* spp. in alcids that are now in progress. The nature of this assemblage could not be revealed, however, in the absence of clear morphological limits established for *T. jagerskioeldi*.

Specimens attributable to other nominal species of *Tetrabothrius* occurred in stercorariids, larids, and rarely among alcids as hosts. Multiple species of *Tetrabothrius* (excluding *T. jagerskioeldi* and *Tetrabothrius* n. sp.–undescribed) were found in 218 of all 1,826 avian specimens (prevalence = 12%). *Tetrabothrius* spp. occurred in 26 of 1,334 alcids of 7 species (prevalence = 2%) from 8 of 43 localities and among 192 of 439 specimens of larids and stercorariids (prevalence = 44%) from 15 of 43 localities (Supplementary Data Table 2). Among phalacrocoracids, 53 specimens of 3 species were examined from 8 of 43 localities and none was infected with other *Tetrabothrius* spp. Among stercorariids, 36 specimens of 3 species were examined from 3 of 43 localities; single specimens of *Tetrabothrius* were found respectively in *Stercorarius longicaudus* Vieillot and *S. pomarinus* Temminck during pelagic migration during late summer to early autumn from the eastern North Pacific off the coast of Washington State. Among 403 larids examined, species of *Tetrabothrius* were found in 189 host specimens (47% prevalence; range in intensity= 1–43) representing 7 of 10 species from 15 of 43 localities (Supplementary Data Table 2). Multiple species of *Tetrabothrius* and mixed infections were typical in larid hosts, and provisional assessments indicate a diverse assemblage: *T. erostris*; *T. cylindraceus* Rudolphi, 1819; *T.* cf. *morschitini* Murav'eva, 1968; *T.* cf. *macrocephalus* (Rudolphi, 1808); and additional unidentified specimens (complete characterization of collections in larids and stercorariids is currently deferred).

Specimens attributable to *T.* cf. *erostris* were rarely observed (prevalence < 1.0%) among alcids in the North Pacific inventory collections (Table 4; Supplementary Data Table 2); 6 of 18 alcid species were recognized as hosts. Single specimens were provisionally identified in 2 horned puffins, *Fratercula corniculata* (Naumann), from Buldir Island, and from pelagic habitats of the Western Aleutian Islands, 2 tufted puffins, *F. cirrhata* (Pallas) from Kodiak Island, a common murre, Cassin's auklet and a rhinoceros auklet from pelagic habitats over Grays Marine Canyon, Washington, and a marbled murrelet from Pt. Roberts, Washington (overall intensity= 1–18 cestodes). Additionally, immature (usually scolex only and considerably smaller than the dimensions typical in *T. jagerskioeldi*) or fragmented specimens of *Tetrabothrius* that could not be definitively identified occurred in a spectacled guillemot, *Cepphus carbo* Pallas, from the northern Sea of Okhotsk, common murres from Cape Thompson (1 host) and Kodiak Island (4 hosts), a horned puffin, and 4 tufted puffins from Kodiak Island, and a single tufted puffin from Sitkalidak Island (overall range in intensity = 1–9) (Table 4; Supplemental Data Table 2). Further, as outlined above, *T. jagerskioeldi* was a rare component of the *Tetrabothrius* fauna in northern Laridae, and putative species-level taxa in the *T. jagerskioeldi* complex were not observed in seabird hosts beyond the Alcidae.

Redescription of Tetrabothrius jagerskioeldi

Data from the original descriptions and subsequent redescriptions of *T. jagerskioeldi* and *T. intrepidus* are summarized as a basis for comparisons. These data are augmented by new observations and series of measurements completed during the current study (Table 2; Figures 1–11). All measurements are reported in micrometers unless otherwise indicated. Mensural data are given as ranges with means in parentheses.

Tetrabothrius jagerskioeldi, type series

A partial redescription of *T. jagerskioeldi*, including new data and observations, is based on examination of the original type series of Nybelin (1916) in *Cepphus grylle* and other voucher specimens collected in 1916 and prepared in 1995 (Table 2); symbiotype specimens are unknown.

Table 4. Substantiated Records of Host and Geographic Occurrence for Other Species of *Tetrabothrius* in Alcidae

Parasite Species	Host Species	Geographic Distribution and Source of Record
***Tetrabothrius cylindraceus* Rudolphi, 1819**	*Uria aalge*	Northwestern Atlantic (Threlfall, 1971) ▲
	Uria lomvia	Greenland (Ditlevsen, 1914) ▲
***Tetrabothrius erostris* Lönnberg, 1896**	*Uria aalge*	Northwestern Atlantic (Threlfall, 1971) ▲ Cardignanshire, Wales ❋★ Concarneau, France ❋★ North Sea, Netherlands ❋★ Grays Marine Canyon, Eastern Pacific ❋✪★
	Brachyramphus marmoratus	Pt. Roberts, Washington ❋✪★
	Cepphus grylle	Greenland (Ditlevsen, 1914) ▲ West Greenland (Baer, 1956) ❋
	Cerorhinca monocerata	Grays Marine Canyon, Eastern Pacific ❋✪★
	Fratercula cirrhata	Kodiak Island, Gulf of Alaska ❋✪★
	Fratercula corniculata	Buldir Island, Western Aleutian Islands ❋✪★ Western Aleutian Islands, pelagic habitat ❋✪★
	Ptychoramphus aleuticus	Grays Marine Canyon, Eastern Pacific ❋✪★
***Tetrabothrius macrocephalus* Rudolphi, 1819**	*Brachyramphus marmoratus*	Sakhalin Island, Western North Pacific (Krotov and Deliamure, 1952) ▲
***Tetrabothrius* sp. unidentified**	*Uria aalge*	Northwestern Atlantic (Threlfall, 1971) ▲ Cape Thompson, Chukchi Sea ❋★ Kodiak Island Gulf of Alaska ❋★
	Uria lomvia	Northwestern Atlantic (Muzaffar, 2009) ▲
	Cepphus carbo	Northern Sea of Okhotsk ❋★
	Fratercula cirrhata	Kodiak Island, Gulf of Alaska ❋★ Sitkalidak Island, Gulf of Alaska ❋★
	Fratercula corniculata	Kodiak Island, Gulf of Alaska ❋★

Notes:

▲ Record not substantiated by archived specimens.

❋ Record substantiated by permanent archived specimens held in an international museum collection; specimens examined during the current study.

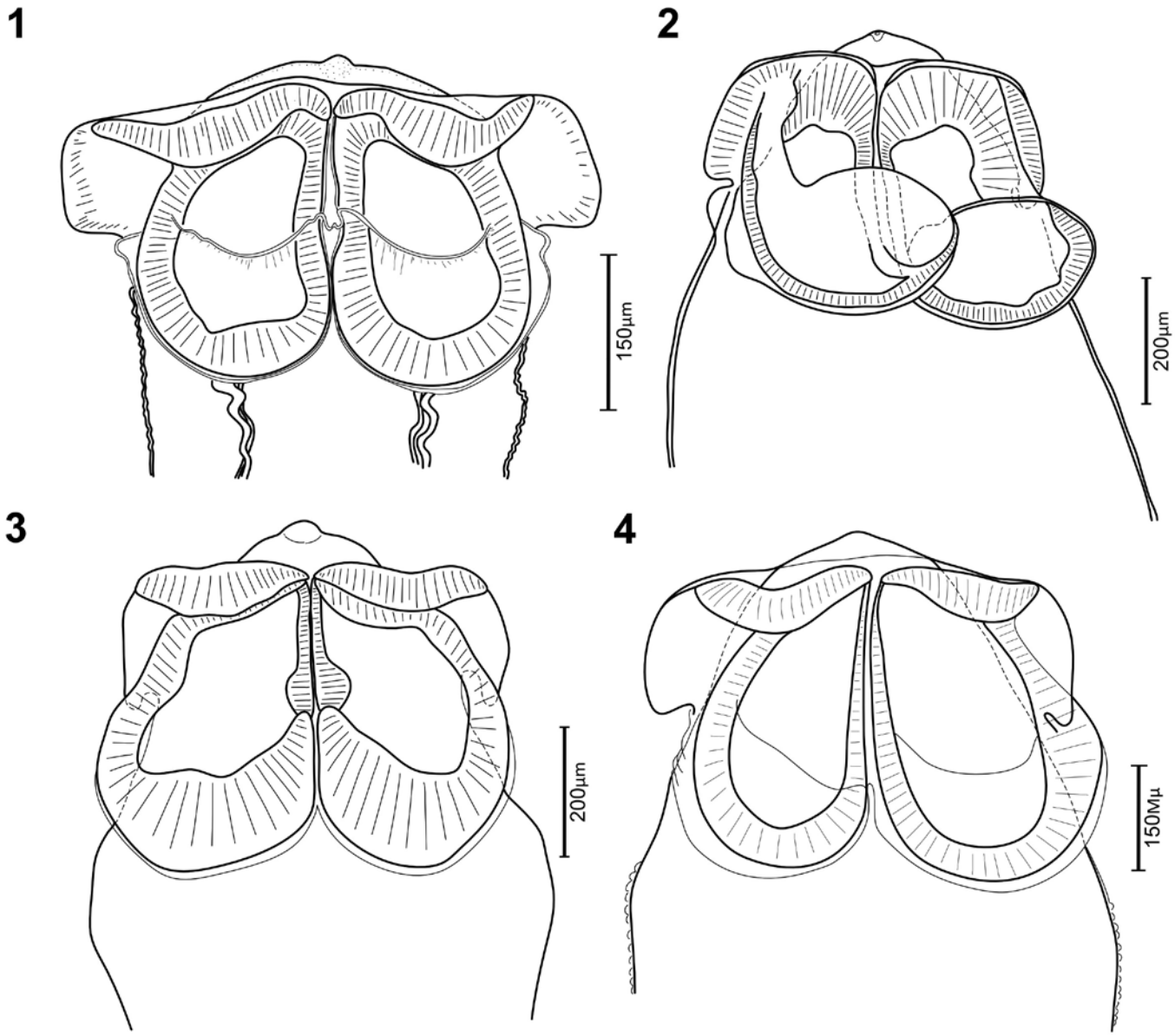
★ New geographic record.

✪ New host record.

***General redescription*:** Robust tetrabothriid cestodes. Total length of strobila undetermined. Craspedote, segments consistently wider than long, 420–500 × 1,400–1,660 in maturity, length:width ratio 1:2.8–3.95. Scolex highly muscularized, 325 long × 430 wide; with 4 prominent bothridia 285–300 long × 195–215 wide; 4 auricles strongly developed. Neck region short to absent. Genital pores unilateral, dextral in dorsal view, with lip-like margin at orifice. Osmoregulatory canals well developed; dorsal system 6.5–26 in diameter; ventral system 16–44, with single transverse canal, lacking multiple anastomoses. Genital ducts passing between dorsal and ventral osmoregulatory canals.

***Longitudinal musculature*:** Musculature prominent in transverse sections of proglottids; inner and outer bundles arranged in single layers. In maturity, inner bundles large in diameter,118–125 in number, 5–53 fibers per bundle; outer bundles relatively small in diameter; 202–221 in number; 3–12 fibers per bundle. Numbers of muscle bundles maximum in mature to gravid proglottids.

***Male system*:** Protandrous, ontogeny of male system not determined. Testes situated in 2–3 layers, surrounding female organs, and slightly overlapping ovary along posterior margin; (n = 27 segments, immature to early mature) 46–58 (52) in number; (n = 20) 39–78 (62)



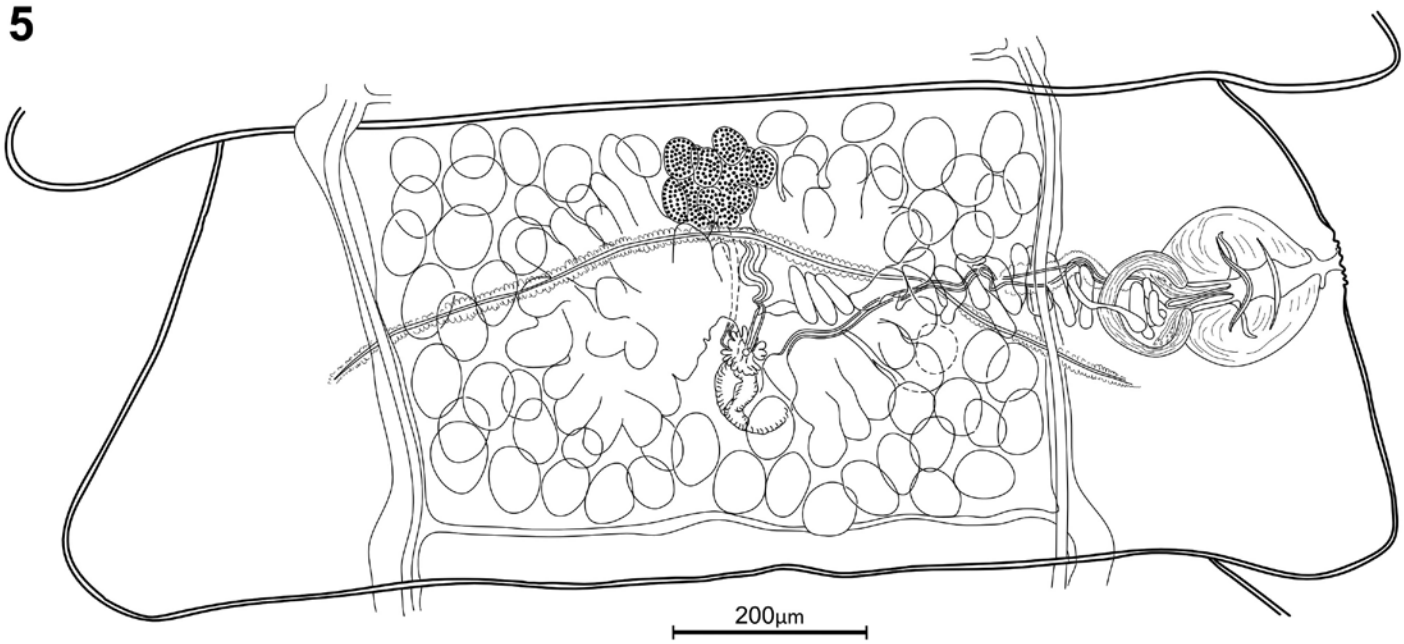
Figures 1–4. *Tetrabothrius jagerskioeldi*, showing structural consistency of scolex in specimens from localities and hosts across the North Atlantic and North Pacific.

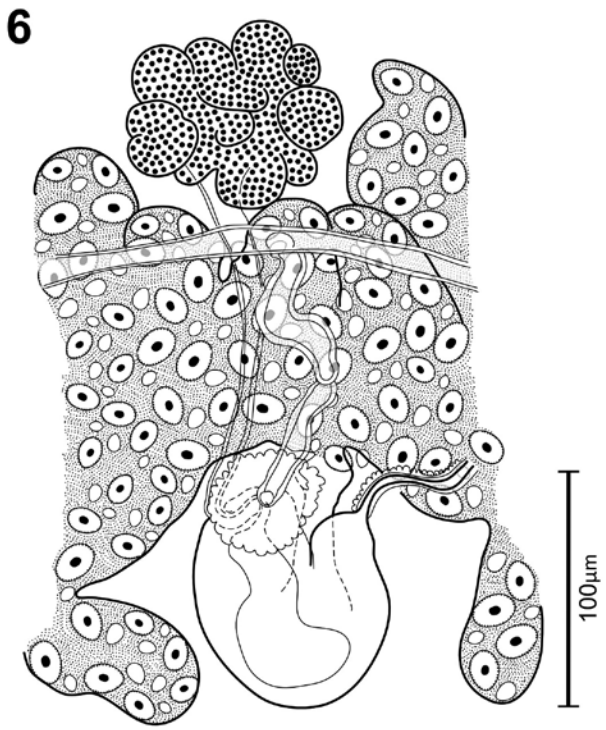
Fig. 1. Specimen from voucher series of Nybelin (1916) in *Cepphus grylle* from Väderöarna, Sweden (Nybelin 1916-2915). Note well-developed auricular appendages and muscular bothridia. Presence of apical vestigial pedicle indicates this was a recent infection and the specimen had developed to the early mature stage.

Fig. 2. Holotype specimen of *Tetrabothrius intrepidus*, attributed to Baylis (1919) in *Cepphus grylle* from "Yukanski," Kola Peninsula, Russia (British Museum Natural History, BMNH 1919.6.14.24).

Fig. 3. Voucher specimen originally attributed to *T. intrepidus* in *Cepphus grylle* from Reykjavik, Iceland (Museum d'Histoire Naturelle, Geneva, MHN No. 65/73).

Fig. 4. Voucher specimen attributed to *Tetrabothrius jagerskioeldi* in *Uria aalge* from Shuyak Island, Alaska (R. L. Rausch Field Collection No. 13473; MSB Catalogue No. 5732).





Figures 5–6. *Tetrabothrius jagerskioeldi*, type specimen in *Cepphus grylle* from Bohuslän, Kristineberg, Sweden, on 28 July 1910 (Nybelin 28-VII-1910; specimen held in Naturhistoriska Museet, Göteborg, Sweden).

Fig. 5. Mature proglottid, dorsal view in whole mount. Note dextral placement of genital pore; position of genital ducts and transverse uterine stem between osmoregulatory canals; and strongly compact, globular vitelline gland.

Fig. 6. Female genital organs and ducts in whole mount, dorsal view. Note relative positions of the ventral vitelline gland and single descending duct, posterior inner seminal receptacle ventral to the ovarian isthmus and Mehlis' gland, and the dorsal ascending uterine duct and transverse uterine stem.

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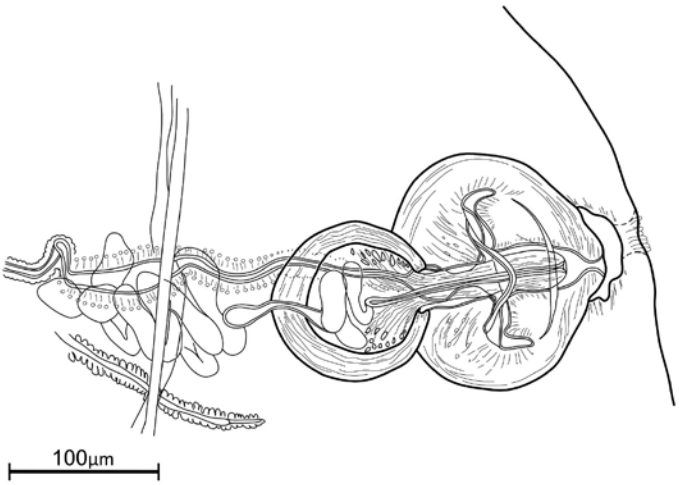

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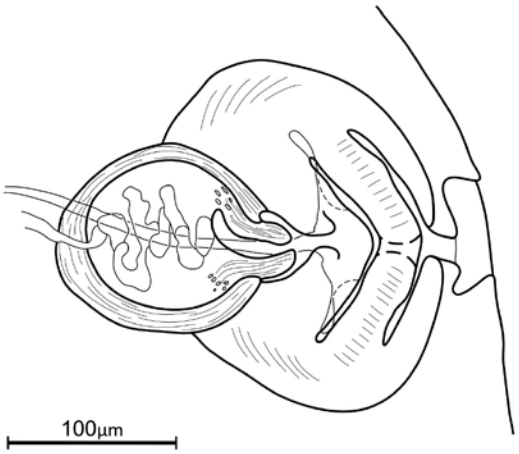

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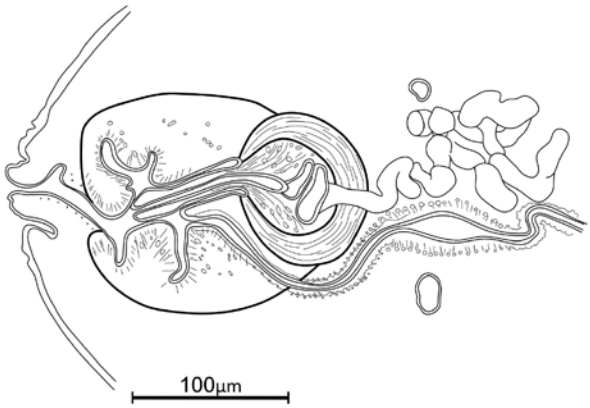

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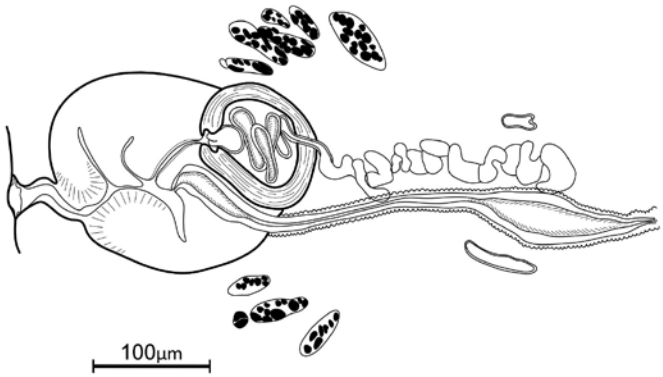

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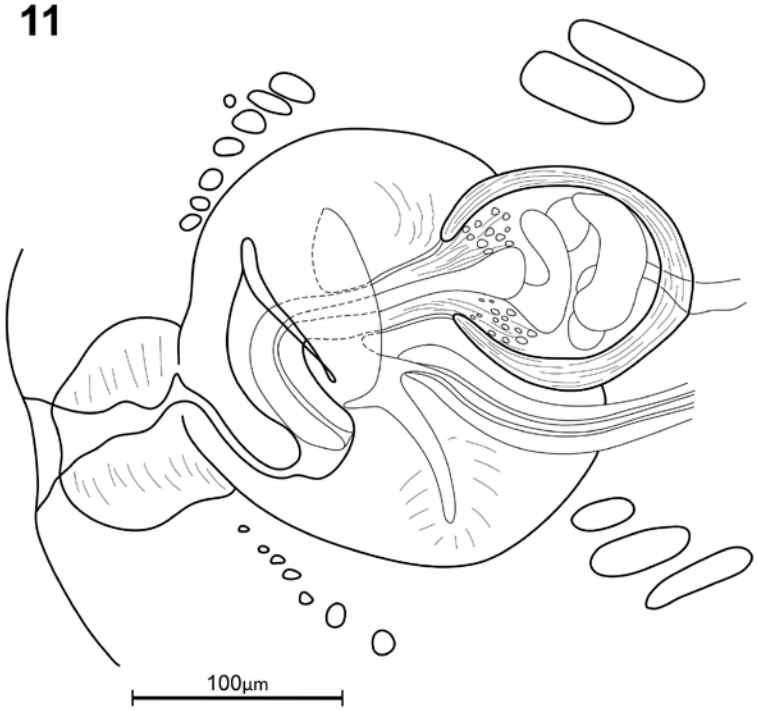

Figures 7–11. *Tetrabothrius jagerskioeldi*, showing structural consistency of genital atrium in lateral view from transverse sections and in whole mounts from the type series and other specimens from the North Atlantic and North Pacific.

Fig. 7. Genital atrium in dorsal view from whole mount of mature type specimen of Nybelin (1916). Note muscular genital atrium and cirrus sac, with orifice of male canal opening through prominent triangular papilla and bordered by muscular dorsal bar.

Fig. 8. Genital atrium in dorsal view from whole mount in pregravid voucher specimen attributed to *T. intrepidus* (Museum d'Histoire Naturelle, Geneva, MHN No. 65/72). Note prominent dorsal genital papilla and porad position of muscular dorso-lateral bars.

Fig. 9. Genital atrium, lateral view from anterior, in transverse thin-section of mature type specimen of Nybelin (1916). Note muscular aspect of atrium containing relatively straight male canal with strongly muscular cirrus sac and gently curving female canal with weak dilatation distally. Genital ducts pass between the dorsal and ventral osmoregulatory canals, with spindle-shaped vaginal seminal receptacle ventral to convoluted and voluminous vas deferens.

Fig. 10. Genital atrium, lateral view from anterior in transverse, hand-cut, thick section of pregravid specimen in type series of *T. intrepidus* (British Museum of Natural History, BMNH 1919.6.14.24). Note position of genital atrial canals opening relative to dorsal papilla, position of dorsal bars, and distal expansion of terminal female canal. Voluminous vas deferens and spindle-shaped vaginal seminal receptacle pass between the poral osmoregulatory canals. Position and structure of large inner muscle bundles in depicted.

Fig. 11. *Tetrabothrius jagerskioeldi*, genital atrium lateral view from anterior, in transverse, hand-cut thick section of late mature region of strobila of voucher specimen in *Uria aalge* from Shuyak Island, Alaska (R. L. Rausch No 13473, slide 1-B/MSB Catalog 5732). Note position of genital ducts, massive cirrus sac, and cirrus opening through prominent papilla bordered by dorso-ventrally directed muscular bars. Positions of the inner and outer muscle bundles are depicted.

in greater diameter in mature proglottids. Cirrus pouch diameter in early mature to mature (n = 25) 70–114 (94); in gravid (n = 3) 96–104. Vas deferens highly convoluted, voluminous. Cirrus pouch with thick wall, 16–21 in mature segments. Genital atrium diameter in early mature to mature (n = 25) 117–177 (140); in gravid (n = 3) 153–169. Male genital canal contained within atrial wall, straight to weakly curved, opening through single, rounded, broadly triangular papilla situated in dorsal aspect of genital atrium with vaginal orifice at base; triangular structure of papilla visible in dorsal or ventral view of atrium in whole mount. Dorsal bar situated porad of male papilla in whole mount view of atrium, appearing as lateral processes extending from dorsal to ventral bordering termination of male canal in transverse thick section. Length of male canal in mature proglottids (n = 14) 39–57 (46), (n = 3) in gravid 44–49 as determined in transverse section.

***Female system*:** Center of female organs primarily on midline of proglottid. Ovary bilobed, (n = 8) 410–600 (534) wide in mature proglottids. Vitelline gland compact, globular, (n = 15) 101–192 (136) wide × 44–120 (85) long in mature segments, situated anteroventral to ovary, with single duct extending ventral to ovary to join uterine duct in Mehlis' gland. Mehlis' gland, (n = 10) 44–57 (52) in diameter, on midline posterior to ovary. Inner seminal receptacle appearing as dilated region of vagina, (n = 5) 68–91 (81) in diameter, lateral and adjacent to Mehlis' gland. Vagina relatively straight, parallel, ventral to vas deferens. Vaginal seminal receptacle relatively small, with thickened glandular epithelium, crossing between poral osmoregulatory canals, as elongate, spindle-shaped dilatation delimited by sphincters, (n = 10) 52–104 (78) in length. Female canal situated ventral to male canal in genital atrium, with minimal dilatation adjacent to vaginal orifice, entering wall of genital atrium with slight curve, parallel to cirrus sac and male canal; 2 small lobes bordering vaginal aperture in dorso-ventral view. Uterus visible initially as narrow transverse tube extending dorsal to ovary, ventral to vas deferens and testes; extending between poral and antiporal osmoregulatory canals. Not dilated in maturity, expanded in pregravid condition, sacculate in gravid segments. Mature eggs obscure, dorsal uterine pore not observed.

Tetrabothrius intrepidus, type series

A partial redescription is based on examination of type specimens of *T. intrepidus* Baylis, 1919 in *Cepphus grylle*, additional specimens prepared in 1995 from the type series, and a specimen in *C. grylle* from Reykjavik, Iceland (Table 2); symbiotype specimens are unknown.

***General*:** Robust tetrabothriid cestodes. Total length of strobila undetermined. Craspedote, segments consistently wider than long, 700–730 long × 3.5–4.0 mm wide in gravid strobila, length:width ratio 1:5.0–5.5. Scolex highly muscularized, 461–550 long × 597–650 wide;

with 4 prominent bothridia 371–500 long × 310–335 wide; 4 auricles strongly developed. Apical pedicle present on scolex. Neck region short to absent. Genital pores unilateral, dextral in dorsal view, with liplike margin at orifice. Osmoregulatory canals well developed. Genital ducts passing between dorsal and ventral osmoregulatory canals.

***Longitudinal musculature*:** Musculature prominent in transverse sections of proglottids.

***Male system*:** Ontogeny of male system could not be determined. Number of testes not be determined. Cirrus pouch diameter in pregravid to gravid segments (n = 17) 96–130 (109). Vas deferens highly convoluted, voluminous. Cirrus pouch with thick wall, 13–26 in pregravid segments. Genital atrium diameter in pregravid to gravid segments (n = 15) 143–239 (192); in gravid (n = 3) 153–169. Male genital canal contained within atrial wall, straight to weakly curved, opening through single, rounded, broadly triangular papilla situated in dorsal aspect of genital atrium with vaginal orifice at base. Dorsal bar situated porad of male papilla in whole mount view of atrium, appearing as lateral processes extending from dorsal to ventral bordering termination of male canal in transverse thick section. Length of male canal in pregravid proglottids (n = 7) 44–55 (51) as determined from examination of transverse sections.

***Female system*:** Center of female organs primarily on midline of proglottid. Ovary bilobed, becoming diffuse in pregravid proglottids. Vitelline gland compact, globular, situated anteroventral to ovary, with single duct extending ventral to ovary, (n = 3) 182–208 wide in pregravid. Mehlis' gland on midline posterior to ovary. Inner seminal receptacle not determined. Vagina relatively straight parallel, ventral to vas deferens. Vaginal seminal receptacle relatively small, with thickened glandular epithelium, crosses between poral osmoregulatory canals, as elongate, spindle-shaped dilatation demarcated by sphincters, 117–122 in length. Female genital canal, relatively straight, disposed ventral and parallel to male genital canal in genital atrium, with minimal dilatation adjacent to vaginal orifice. Uterus saccate when gravid, extending between poral and antiporal osmoregulatory canals; dorsal uterine pore on midline at anterior margin of gravid proglottids. Eggs with irregular hyaline capsule containing embryophore (n = 20) 22–37 (26) long × 30–41 (36) wide. Oncosphere (n = 20) 18–23 (20) long × 25–33 (30) wide; lateral embryonic hooks (n = 40) 12–15 (14) long; medial embryonic hooks (n = 20) 14–15 (15) long.

***Tetrabothrius jagerskioeldi* (North Pacific Specimens in Alcidae)**

A redescription is based on examination of 20 specimens of *T. jagerskioeldi* in 14 avian hosts and 6 host species among Alcidae from localities of North Pacific origin (Table 2; Supplementary Data Table 2 and Supplementary Data Table 3). Identity of these specimens was confirmed based on direct comparisons to the type series for *T. jagerskioeldi*.

***General redescription*:** Large, robust tetrabothriids; maximum length of strobila 85–203 mm. Segments wider than long throughout strobila; (n = 19) 275–675 (445) × 1,625–3,125 (2,172) in mature; (n = 12) 375–775 (550) × 1,825–3,375 (2,566) in pregravid; maximum observed (n = 13) 525–1,075 (747) × 2,230–3,900 (2,784) in gravid. Length:width ratio in mature 1:4.9–5.1; in pregravid, 1:4.96–5.09; in gravid 1:2.44–4.73. Scolex rectangular, wider than long (n = 16) 350–580 (489) long × 490–700 (580) wide; auricles prominent. Bothridia well developed, (n = 24) 240–500 (406) long × 235–370 (277) wide, with muscular margins. Apical region with slight rounded expansion; often with vestigial pedicle of apical sucker. Neck relatively short. Ventral osmoregulatory canals large in diameter; single transverse canal without anastomoses; dorsal canals narrow. Genital pores unilateral, dextral, situated marginally in middle third of proglottid. Genital ducts and extensions of transverse uterus pass between poral osmoregulatory canals.

***Longitudinal musculature*:** Musculature prominent in transverse sections of proglottids; inner and outer bundles arranged in single layers. Inner bundles large in diameter; (n = 8) 99–146 (114) in number; (n = 20) 6–37 (19) fibers per bundle. Outer bundles relatively small in diameter; (n = 8) 185–237 (204) in number; (n = 20) 3–11 (7.0) fibers per bundle. Numbers of muscle bundles maximum in mature proglottids, diminishing in number posteriad in post-mature and gravid segments.

***Male system*:** *Genital anlagen* visible immediately posterior to neck. Testes positioned dorsally in 2–3 layers surrounding and partially overlapping female organs. Testes (n = 54 segments from 7 strobila) 40–70 (54) in number counted in immature to early mature segments. Vas deferens prominent, highly convoluted, distended adjacent to poral osmoregulatory canals. Cirrus sac ovoid, situated in dorsal aspect of genital atrium, increasing in diameter posteriad, attaining maximum dimensions in gravid segments; diameter (n = 111) 65–110 (88) in mature, (n = 109) 75–130 (93) in pregravid, (n = 44) 78–152 (106) in gravid. Cirrus sac with thickened muscular wall 15–25. Cirrus sac contains extension

of convoluted vas deferens and cirrus armed with miniscule but prominent spines. Genital atrium ovoid, structurally consistent with Nybelin and Baylis type series, highly muscularized, attaining maximum dimensions in gravid segments; (n = 47) 125–190 (154) in mature, (n = 55) 112–230 (169) in pregravid, (n = 20) 142–205 (177) in gravid. Male genital canal, dorsal, extending through wall of atrium, straight to weakly curved ventrally, opening on ventral aspect of prominent triangular male papilla in center of atrial lumen; sphincters not observed. Length of male canal increases with age of proglottid and development of genital atrium; (n = 10) 41–50 (45) long in maturity; (n = 48) 37–62 (47) in late mature to pregravid segments.

***Female system*:** Ovary multilobate, with 2 prominent wings, situated in anterior 2/3 of segment with center of female organs on midline; not extending to osmoregulatory canals; (n = 58) 450–980 (689) in maximum width in mature segments, (n = 20) 420–900 (708) in pregravid. Vitelline gland, compact, globular, (n = 60) 120–400 (202) wide × 48–170 (108) long in mature, (n = 25) 120–280 (208) × 70–140 (105) in pregravid; situated anteroventral to ovary, with center of organ on midline; with single broad common vitelline duct passing ventral to ovary. Common vitelline duct extends posteriad to join uterine duct enclosed within Mehlis' gland ventral to ovary. Vagina terminates proximally as thin-walled, ellipsoidal inner seminal receptacle; extends porad as thin tube ventral to testes, dorsal to ovary. Vaginal seminal receptacle present as elongate, spindle-shaped dilatation, demarcated by sphincters at the level of the poral osmoregulatory system; maximum length (n = 10) 100–157 (132) in mature, (n = 20) 100–170 (127) in pregravid segments, attained adjacent to but not overlapping poral wing of ovary. Distal vagina with thickened muscular wall, enters genital atrium ventral to cirrus sac, parallel to male genital canal, opening ventrally near base of male papilla; region of distal vagina within atrial wall minimally expanded as atrial seminal receptacle; atrial vagina spinose. Ascending uterine stem extends anteriad from dorsal aspect of Mehlis' gland; transverse tubular uterine stem initially visible coinciding with ovarian development. Mature uterus, a broad sacculate structure lined with cellular epithelium, situated dorsally in proglottid, extending between osmoregulatory canals. Uterine pore median, dorsal, patent in pregravid strobila; segments anapolytic. Mature eggs contained within capsule and granular membrane (n = 10) 65–82.5 (73) in diameter. Hyaline embryophore (n = 10) 27.5–35 (29.5) long × (n = 21) 34–42.5 (39) wide; containing oncosphere (n = 40) 20–26 (23) long × 27.5–39 (32) wide. Embryonic hooks similar in structure and dimensions, (n = 17) 12.5–17.5 (15) long for medial pairs, (n = 19) 15–17.5 (15.5) for lateral groups.

Host Species: *Brachyramphus marmoratus* (Gmelin), *Cepphus carbo* Pallas, *Cepphus columba* Pallas, *Cepphus grylle* (Linnaeus), *Cerorhinca monocerata* (Pallas), *Uria aalge* (Pontoppidan).

Voucher Specimens in Alcidae, North Pacific Basin: Museum of Southwestern Biology, Parasitology Division—MSB PARA—1738, 3990, 4046, 5732, 26828, 27879, 27880, 27912, 27916, 27919, 27927, 27928, 29234, 28951. (See Table 2 and Table 3 including new data for host and geographic distributions; Supplementary Data Table 2; Supplementary Data Table 3).

Symbiotype Specimens: Unknown.

Tetrabothrius jagerskioeldi (North Pacific Specimens in Laridae and Phalacrocoracidae)

A partial redescription is based on examination of 29 specimens of *T. jagerskioeldi* in 14 individuals of *Larus glaucescens* hosts and 1 specimen in *Urile pelagicus* from North Pacific localities (Table 2; Supplementary Data Table 2 and Supplementary Data Table 3). Identity of these specimens was confirmed based on direct comparisons to the type series and to specimens recovered in Alcidae hosts from the North Pacific Basin.

***General redescription*:** Large, robust tetrabothriids; maximum length of strobila 101–158. Segments wider than long throughout strobila; (n = 4), width 1,618–3,348 (2,497) in mature; (n = 4) 2,560–3,710 in pregravid; maximum observed (n = 11) 2,817–4,540 (3,645) in gravid. Scolex rectangular, wider than long (n = 25) 393–632 (512) long × 477–786 wide; auricles prominent. Bothridia well developed. Apical region with slight rounded expansion; often with vestigial pedicle of apical sucker. Neck relatively short. Ventral osmoregulatory canals large in diameter; single transverse canal without anastomoses; dorsal canals narrow. Genital pores unilateral, dextral, situated marginally in middle third of proglottid. Genital ducts and extensions of transverse uterus pass between poral osmoregulatory canals.

Longitudinal musculature: Prominent in transverse sections of proglottids; inner and outer bundles arranged in single layers. Inner bundles large in diameter; (n = 14) 60–104 (84) in number. Outer bundles relatively small in diameter; (n = 14) 143–184 (172) in number.

Male system: *Genital anlagen* visible immediately posterior to neck. Testes positioned dorsally in 2–3 layers surrounding and partially overlapping female organs.

Testes (n = 174 segments from 21 strobila) 40–73 (55) in number counted in immature to early mature segments. Vas deferens prominent, highly convoluted, distended adjacent to poral osmoregulatory canals. Cirrus sac ovoid, situated in dorsal aspect of genital atrium, increasing in diameter posteriad, attaining maximum dimensions in gravid segments; diameter (n = 345) 60–119 (91) in mature, (n = 181) 88–126 (107) in pregravid, (n = 68) 91–132 (110) in gravid. Cirrus sac with thickened muscular wall. Cirrus sac contains extension of convoluted vas deferens and cirrus armed with miniscule but prominent spines. Genital atrium ovoid, structurally consistent with Nybelin and Baylis type series, highly muscularized, attaining maximum dimensions in gravid segments; (n = 79) 95–203 (159) in mature, (n = 43) 155–238 (194) in pregravid, (n = 20) 145–215 (175) in gravid. Male genital canal, dorsal, extending through wall of atrium, straight to weakly curved ventrally, opening on ventral aspect of prominent triangular male papilla in center of atrial lumen; sphincters not observed. Length of male genital canal showing limited variation with age of proglottid and development of genital atrium; (n = 55) 36–65 (52) long in maturity; (n = 27) 34–60 (52) in late mature to pregravid segments.

Female system: Ovary multilobate, with 2 prominent wings, situated in anterior 2/3 of segment with center of female organs on midline; not extending to osmoregulatory canals; (n = 69) 560–1,251 (810) in maximum width in mature segments; (n = 37) 838–1,335 (1,110) in pregravid. Vitelline gland, compact, globular, (n = 100) 107–345 (198) wide × 52–155 (107) long in mature, (n = 53) 179–370 (284) wide in pregravid; situated anteroventral to ovary, with center of organ on midline; with single broad common vitelline duct passing ventral to ovary. Common vitelline duct extends posteriad to join uterine duct enclosed within Mehlis' gland ventral to ovary. Vagina terminates proximally as thin-walled, ellipsoidal inner seminal receptacle; extends porad as thin tube ventral to testes, dorsal to ovary. Vaginal seminal receptacle present as elongate, spindle-shaped dilatation, demarcated by sphincters at the level of the poral osmoregulatory system. Distal vagina with thickened muscular wall, enters genital atrium ventral to cirrus sac, parallel to male genital canal, opening ventrally near base of male papilla; region of distal vagina within atrial wall minimally expanded as atrial seminal receptacle; atrial vagina spinose. Ascending uterine stem extends anteriad from dorsal aspect of Mehlis' gland; transverse tubular uterine stem initially visible coinciding with ovarian development. Mature uterus, a broad sacculate structure lined with cellular epithelium, situated dorsally in proglottid, extending ventrally beyond and between poral and antiporal osmoregulatory canals. Uterine pore median, dorsal, patent in pregravid strobila; segments anapolytic. Mature eggs contained within capsule and granular membrane. Hyaline embryophore containing oncosphere (n = 64) × 21–31 long × (n = 83) 29–44 (36) wide. Embryonic hooks similar in structure and dimensions, (n = 39) 12.5–18 (15.5) long for medial pairs, (n = 39) 12.5–18 (16) for lateral groups.

Host Species: *Larus glaucescens* (Naumann), *Urile pelagicus* (Pallas).

Voucher Specimens in Laridae and Phalacrocoracidae, North Pacific Basin: Museum of Southwestern Biology, Parasitology Division—MSB PARA—27910, 27871, 27872, 27873, 27874, 27875, 27876, 27883, 27886, 27890, 27894, 27898, 27902, 27905, 27908. (See Table 2 and Table 3 including new data for host and geographic distributions; Supplementary Data Table 2, Supplementary Data Table 3).

Symbiotype Specimens: Unknown.

Remarks—Defining Morphological and Species Diversity

Specimens of *T. jagerskioeldi* are diagnosed by a characteristic configuration of the genital atrium, position of the male and female genital canals, structure of the male and female organ systems, and numbers of testes (Figures 1–11; Table 2). The marginal genital atrium, dextral in position, and observed in dorso-ventral view, is defined by a prominent, dorsally situated, triangular papilla with the aperture of the male canal opening centrally near the base and female canal adjacent and ventral in position. In transverse section, lateral processes extend ventrally from the dorsal aspect of the genital atrium bordering the anterior edge of male genital papilla. The vagina is relatively straight entering the wall of the genital atrium and slightly curved in parallel to the cirrus sac and male canal. The genital ducts and transverse uterine stem pass between the poral osmoregulatory canals; the uterine stem passes between the antiporal canals. The transverse ventral osmoregulatory canal lacks multiple anastomoses. The vaginal seminal receptacle occurs as a spindle-shaped expansion with a prominent epithelium, demarcated by sphincters, at the level of the poral canals. The center of the female organ system (vitelline gland and bi-winged, multilobate ovary, Mehlis' gland) is aligned with the midline of the proglottid. The vitelline gland is strongly compact, globular, and with a

single descending duct. Testes only exceptionally exceed 60 in number; maximum observed in confirmed specimens = 70–73, minimum = 40; mean number in specimens from alcids or larids is about 55.

A suite of characters from original descriptions (and new specimen-based observations from the type series) of *T. jagerskioeldi* and the junior synonym *T. intrepidus* consistently establish identity (Nybelin, 1916; Baylis, 1919). Morphologically, specimens examined from the North Pacific inventory are structurally indistinguishable from the type series, particularly with respect to the configuration of the genital atrium (Figures 1–11; Table 2). The genital atrium remains among the most diagnostically important characters for identification across genera and species of Tetrabothriidae. Defining the limits for structural and meristic characters within species requires a series of measurements and observations that account for ontogeny of male and female genital systems with respect to progressive development of the strobila (Murav'eva and Popov, 1976; Hoberg, 1987; Hoberg et al., 1991).

An understanding of the morphological limits for *T. jagerskioeldi* derived from a large series of geographically disparate specimens has direct implications for documenting parasite diversity. Correct identification of all cestodes included in redescriptions outlined in monographs by Baer (1954) and Temirova and Skrjabin (1978) may be equivocal, as specimens are no longer available for verification, and detailed data for field collections were not generally presented (Table 2). Considering meristic data in these monographs, it is apparent that some, but not all, specimens would have represented *T. jagerskioeldi*. Figures of the genital atrium presented for *T. jagerskioeldi* by Baer (1954) at a minimum indicate some component of Nybelin's mounted histological sections and type specimens had been evaluated. It is not clear, however, that other specimens were examined from a broader range of alcid hosts (*Alca torda* and *Uria aalge*) that were reported in the monograph. Thus, later misidentification of *T. jagerskioeldi* from localities in West Greenland is problematic. Baer (1956) reported this species in *Alca torda* (specimens consistent with *T. erostris*) and *Cepphus grylle* (consistent with an undescribed species), and this is a case in which identity of voucher specimens held in Museum d'Histoire Naturelle, Geneva, could be verified.

Temirova and Skrjabin (1978) examined, redescribed, and completed a series of figures attributed to *T. jagerskioeldi* from specimens likely to have been originally collected by Belopol'skaia (1952) from the Seven Islands Reserve in Arctic Russia. Included were specimens in parasitic jaeger, *Stercorarius parasiticus* (Linnaeus), and cestodes in *Cepphus grylle*, *Alca torda*, and *Fratercula arctica* (Linnaeus). As depicted in a series of published figures, the presence of a massive domelike apical expansion of the scolex, apparent ventral position of the genital ducts, relative width of the vitelline gland (elongate), and the large diameter of the genital atrium in at least some of these specimens are inconsistent with the Göteborg type series and North Pacific specimens of *T. jagerskioeldi*. We suggest that the redescription outlined by Temirova and Skrjabin (1978) is a composite, which includes *T. jagerskioeldi* and at least one currently undescribed species of *Tetrabothrius*. Our contention, however, cannot be directly evaluated as the collections assembled by Belopol'skaia (1952) were accidentally destroyed.

The identity of *T. jagerskioeldi* and consequently the published host ranges remain problematic and, in some cases, unsubstantiated as a considerable number of records based on field collections can no longer be linked directly to specimens (e.g., Ditlevsen, 1914; Krotov and Deliamure, 1952; Belopol'skaia, 1952, 1963a, 1963b; Threlfall, 1971; Smetanina, 1979, 1981; Temirova and Skrjabin, 1978; Smetanina and Leonov, 1984) (Table 3). The documentation of host occurrence was seldom validated through identified parasite specimens that were archived. Host and geographic distributions are further confounded now by a cryptic complex of species that is recognized in our current study of available specimens (Table 3; Supplementary Table 2).

Defining a Species Complex in *T. jagerskioeldi*

Based on the spectrum of characters we explored, it was apparent that numerous specimens of *Tetrabothrius* among genera and species of Alcidae from the North Pacific inventory could not be accommodated in *T. jagerskioeldi* (Table 3; Table 5; Supplementary Data Table 2). Superficially, these are all large and robust tapeworms referable to *Tetrabothrius*, potentially contributing to misidentifications and misattribution that have occurred both in the literature and in the few archived specimens in museums (BMNH and MHN) as revealed in our current study. An array of qualitative (structural) and quantitative attributes partitioned among these specimens are discordant with *T. jagerskioeldi* but concurrently exhibit considerable stability with respect to geographic and host distributions (Table 3; Table 5). A complex of otherwise cryptic and undescribed species minimally involving

Table 5. Characters That Are Discordant with *Tetrabothrius jagerskioeldi* Nybelin, 1916

- Scolex structure and dimensions
- Structure of the osmoregulatory canals
- Structure of genital atrium, including papilla(e), position, direction and length of the male and female canals, dilatations of the atrial vagina
- Structure and position of the distal vagina near junction with genital atrium
- Structure and dimensions of the vitelline gland; structure of descending vitelline duct(s)
- Position of genital ducts and transverse uterine stem relative to osmoregulatory canals
- Structure and position of the vaginal seminal receptacle
- Position of female organs relative to the midline of the proglottid
- Position of the genital pore
- Numbers of testes

3–4 additional taxa contained within *T. jagerskioeldi* is indicated (Table 3; Supplementary Data Table 2); these are designated a *Tetrabothrius* undescribed n. sp. in our current study. The details and taxonomic decisions that will emerge from these observations are deferred for ongoing studies defining diversity in the marine fauna. Some salient points, however, regarding recognition of a species complex are outlined in the subsequent section.

Discussion

Hoberg (1984) and Muzaffar and Jones (2004) summarized data for diversity of helminths including species of *Tetrabothrius* among Alcidae derived from the published record outlined in the literature. Both reviews were based on assumptions of a single species of large, robust tapeworm, namely *T. jagerskioeldi*, as the predominant representative of *Tetrabothrius* in alcid hosts. Hoberg (1984) did not provide species-level identification for specimens in alcids from the North Pacific at that time; those collections are now under evaluation in our current study.

Historically *Tetrabothrius jagerskioeldi* has been considered a typical or characteristic parasite across a broad diversity of seabirds among the Alcidae (Charadriiformes) (e.g., Fuhrmann, 1932; Joyeaux and Baer, 1936; Belopol'skaia, 1952; Baer, 1954; Yamaguti, 1959; Temirova and Skrjabin, 1978; Schmidt, 1986; Mariaux et al., 2017). Records from hosts beyond the Alcidae have not been reported except for those in parasitic jaegers from the Seven Islands Reserve by Belopol'skaia (1952), and specimens in glaucous-winged gulls and a pelagic cormorant in our study. None of these definitive monographs have a foundation established by the deposition of archival vouchers in various international collections. Other species, including *T. cylindraceus*, *T. erostris*, and *T. macrocephalus* have sporadically been reported in alcids (Temirova and Skrjabin, 1978; see reviews in Hoberg, 1984; Muzaffar and Jones, 2004) (Table 4). These are readily distinguished from *T. jagerskioeldi* based on the dimensions of the scolex, numbers of testes, and specific attributes of the genital atrium and cirrus sac (e.g., Baer, 1954; Temirova and Skrjabin, 1978). Reports of occurrence and distribution over the past century (now including original records and corrections outlined in our study) recognize 4 nominal species of *Tetrabothrius* in as many as 14 host species among the 24 extant Alcidae (Table 3, Table 4); 6 alcid host species are validated for *T. jagerskioeldi* by archived voucher specimens in our study (Table 3; Supplementary Data Table 2). Further, 14 alcid species are identified as hosts for an assemblage of 3–4 cryptic and currently undescribed species constituting a complex within *T. jagerskioeldi*.

A clear definition of *T. jagerskioeldi* derived from our current evaluations and the recognition of an apparent complex of species (Table 3; Supplementary Data Table 2) brings to question the reliability of identifications that have been outlined in the literature. The absence of archived voucher specimens further renders it impossible to adequately evaluate almost all prior reports that otherwise would document the host range and geographic distribution of *T. jagerskioeldi* and other species of *Tetrabothrius*. Some records, linked to redescriptions, may be correct as outlined in Table 2, but there is now no mechanism for assessing their validity. It is important to note that in instances for which vouchers had been archived for putative specimens of *T. jagerskioeldi* or *T. intrepidus*, many of those identifications have been shown to be incorrect (e.g., Baer (1956)—specimens in *Alca torda* and *Cepphus grylle* from West Greenland and archived museum specimens in *U. aalge* from France, the Netherlands, and Wales).

Exploring Host Range for *T. jagerskioeldi* and *Tetrabothrius* spp.—The North Pacific Inventory

Inventory from localities spanning the North Pacific during a 40-year period from the early 1950s to the early 1990s, as outlined in our study, constitutes the first geographically extensive, specimen-based, and archived collections to serve as a foundation and baseline for exploring species diversity and distribution (Supplementary Data Table 2). Specimens attributed to *T. jagerskioeldi* from these field collections were morphologically consistent with those examined in the type series from Sweden (Table 2). We confirm six alcid species (*U. aalge*, *C. carbo*, *C. columba* Pallas, *C. grylle*, *B. marmoratus* (Gmelin), *C. monocerata* (Pallas)), a larid (*L. glaucescens*), and a phalacrocoracid (*U. pelagicus*) as hosts encompassing a widespread oceanographic range across the North Pacific basin (Table 3; Supplementary Data Table 2). Although a broad host range is apparent, most validated records are now associated with guillemots, species of *Cepphus*, from the Holarctic.

Specimens of *T. jagerskioeldi* were also recovered from hosts among the Laridae and Phalacrocoracidae during geographically extensive surveys at localities in the North Pacific basin (Hoberg, 1979, 1992; E. P. Hoberg, unpublished data; Supplementary Data Table 2). Morphologically based identification was confirmed for a series of specimens in a pelagic cormorant (Buldir Island) and in glaucous-winged gulls, *Larus glaucescens*. Gulls were collected near Central Island (adjacent to Ugaiushak Island) along the Alaska Peninsula during 1976 (4 of 20 adult gulls examined) and at Puffin Island in Chiniak Bay, Kodiak Island during 1977 (10 of 31 adults examined), both sites in the northern Gulf of Alaska. Overall, 21% of glaucous-winged gulls examined at these 2 localities were infected with specimens attributable to *T. jagerskioeldi*; specimens were not found in 13 glaucous-winged gulls examined at Amchitka Island in the central Aleutian Islands in 1976. Mixed species infections in glaucous-winged gulls, involving *T. jagerskioeldi*, *T.* cf. *cylindraceus*, and *T.* cf. *erostris* and possibly undescribed species of *Tetrabothrius* occurred at these sites in the Gulf of Alaska. Overall prevalence for all species of *Tetrabothrius* at Central Island and at Puffin Island were 100% and 88% respectively, indicating the tetrabothriid fauna among larids at these localities was dominated by species other than *T. jagerskioeldi*.

Additional specimens once considered to represent *T. jagerskioeldi* among alcids are now partitioned among an assemblage of previously unrecognized species, collectively designated here as *Tetrabothrius* undescribed n. sp. Prior to detailed comparative morphological evaluations initiated during our study (and in progress), these series of specimens had been provisionally referred to *T. jagerskioeldi* (Hoberg, 1984; Table 3; Supplementary Data Table 2) and in part to *Tetrabothrius* spp. (e.g., Muzaffar and Jones, 2004). Specimens, including those from the North Pacific inventory and Greenland (Baer, 1956), are partitioned to some degree among 14 species of alcids: Alcini (*U. aalge* and *U. lomvia* (Linnaeus)), Cepphini (*C. grylle* and *C. columba*), Synthliboramphini (*S. antiquus* (Gmelin), *S. scrippsi* (Green and Arnold)), Aethiinae (*A. cristatella* (Pallas), *A. pusilla* (Pallas), *A. pygmaea* (Gmelin), *A. psittacula* (Pallas), *P. aleuticus* (Brandt)), and Fraterculini (*F. corniculata*, *F. cirrhata*, *C. monocerata*). Typically, these were large and robust cestodes, superficially resembling *T. jagerskioeldi*. A cryptic complex with distinct species distinguished by, among other characters, the numbers of testes, attributes of the genital atrium, structure of the genital papilla, position of the genital pore, structure of the vaginal seminal receptacle, and placement of the male and female canals can be defined (Table 5). Historically, the morphological limits for *T. jagerskioeldi* had not been adequately delineated, leading to confusion about the diversity of cestodes that may occur among genera and species of alcids and other marine birds. Host and geographic range for an assemblage of species will be explored in subsequent taxonomic studies and descriptions of the *T. jagerskioeldi* species complex.

Considering a broader faunal assemblage circulating among seabirds, tapeworms consistent with *T. jagerskioeldi* or *Tetrabothrius* undescribed n. sp. were not observed among 477 avian specimens (larids, stercorariids, phalacrocoracids, excluding 14 *L. glaucescens* and 1 *U. pelagicus*) of 13 species from North Pacific collections (Supplementary Data Table 2). Notably sampling involved 165 specimens of the pelagic foraging black-legged kittiwake (*Rissa tridactyla* (Linnaeus)): (1) at Buldir Island in the western Aleutian Islands in 1975 (10 examined, 80% prevalence with other species of *Tetrabothrius*); (2) at Ugaiushak Island in 1976 (35; 46%) and at Kodiak Island in 1977 (50; 48%) from the northern Gulf of Alaska; (3) St. Matthew Island from the central Bering Sea in 1982 (14; 21%); and (4) from Talan Island in the northern Sea of Okhotsk in 1988 (20% in 30 breeding adults, 96% in 26 young of the year birds) (Hoberg, 1979, 1992; E. P. Hoberg, unpublished field data). Specimens of slaty-backed gulls, *Larus schistisagus* Stejneger, at the latter site were also hosts for

multiple species of *Tetrabothrius* (71% in 21 adults, 80% in 5 young of the year) (Hoberg, 1992). A diverse group of larids (overall *Rissa tridactyla* (206 total), *R. brevirostris* (Bruch) (2), *Larus hyperboreus* Gunnerus (13), *L. schistisagus* (27), *L. argentatus* (Pontoppidan) (12), *L. heermani* Cassin (6), *Sterna paradisaea* Pontoppidan (37) and *Xema sabini* (Sabine) (34), *Onychoprion aleuticus* (Baird) (1)) and stercorariids (*S. pomarinus* (14), *S. parasiticus* (4), and *S. longicaudus* (18)), representing sampling from the East Siberian Sea, the Sea of Okhotsk, Bering Sea, Gulf of Alaska and pelagic waters of the Eastern Pacific beyond the continental shelf of Washington State were not infected with *T. jagerskioeldi* (Supplementary Data Table 2). Thus, the occurrence of relatively great prevalence for *T. jagerskioeldi* in 2 populations of glaucous-winged gulls from the northern Gulf of Alaska appears notable and may reflect particular attributes of the marine ecosystem at those localities.

Documenting a *Tetrabothrius* Fauna among Alcidae and Other Seabirds

The actual recognized host range for *T. jagerskioeldi* cannot be confirmed unequivocally because of recognition of a putative complex of cryptic species, possibility of multispecies infections, general absence of archival specimens in museum repositories, and incomplete morphological characterization for tapeworms reported in a diverse assemblage of marine avian species. Historical records or attribution of host occurrence fall into 3 categories: (1) unsubstantiated and without documentation of provenance for geographic source; (2) records with information for host and locality but without a link to specimens and specific details of comparative morphology for parasites, and thus absence of a comparative basis to verify identification; (3) records validated by archival deposition of some or all parasite specimens and comparative morphological assessments (Table 3). In a contemporary context we would expect documentation of species richness and diversity to encompass: (1) archival deposition and biodiversity informatics within an interactive database platform and a permanent museum collection; (2) complete georeferenced field data; (3) parasite specimens prepared and evaluated based on comparative morphology and molecular characterization; (4) archival deposition of comparative morphological and molecular data; and (5) host symbiotype specimens and tissues (see Cook et al., 2016, 2017; Dunnum et al., 2017). The research community, editors, reviewers (as gatekeepers to the literature), and journals have the responsibility to build and maintain these standards (e.g., Hoberg et al., 2009).

Major monographs that explored cestode diversity in avian species and other vertebrate hosts did not include comprehensive and specific data about geographic distributions of parasites (e.g., Zschokke, 1903; Ransom, 1909; Fuhrmann, 1932; Joyeaux and Baer, 1936; Baer, 1954; Yamaguti, 1959; Schmidt, 1986; Temirova and Skrjabin, 1978; Ryzhikov et al., 1985). Following the description by Nybelin (1916), all reported *T. jagerskioeldi* in species lists without direct attribution to original literature (primarily in *Alca torda* and *Cepphus grylle*). Whether or not these represented independent records of occurrence cannot be determined. Additionally, voucher specimens, with few exceptions, were not archived in museum repositories from any published field collections outlined below. Further, some personal collections held by individual investigators following publication were later discarded, destroyed, or lost. Consequently, species identity for cestodes as reported in the literature (excluding the original type series for *T. jagerskioeldi* and *T. intrepidus*) can no longer be verified.

Host range reported in the most recent synoptic monograph for the Tetrabothriidae (Temirova and Skrjabin, 1978) and the most recent published review of faunal diversity (Muzaffar and Jones, 2004) cannot be accurately assessed. Temirova and Skrjabin (1978) reported *T. jagerskioeldi* in a stercorariid (*Stercorarius parasiticus*) and 6 species of alcids (*Uria aalge*, *Cepphus grylle*, *C. carbo*, *Synthliboramphus antiquus*, *Fratercula arctica*, and *F. cirrhata*) and included Chukotka, the Kurile Islands, and Barents Sea as Russian localities; published records of field collections in Chukotka have not been discovered, nor has published documentation for this cestode in tufted puffins. Muzaffar and Jones (2004) reported incomplete and incorrect data for geographic localities and also host species for *T. jagerskioeldi* that cannot be linked to original records (e.g., *F. cirrhata*, *F. corniculata*, *Cepphus Columba*, and *B. marmoratus*). Further, all putative records of *T. jagerskioeldi* from Greenland in any host species cannot be validated (Table 3).

Equivocal host and geographic records have been perpetuated downstream in the literature leading to erroneous concepts for the distribution of diversity. Similar to *T. jagerskioeldi*, prior records of *T. cylindraceus* and *T. erostris* attributed to alcids cannot be easily verified. In this context, Temirova and Skrjabin (1978) reported *T. erostris* in *C. grylle* and *C. columba*. According to Ransom (1909), *U. aalge* was a host for *T. cylindraceus*, a record

which was later repeated extensively (e.g., Fuhrmann, 1932; Joyeaux and Baer, 1936; Yamaguti, 1959; Schmidt, 1986; Temirova and Skrjabin, 1978). Records secondarily attributed to Römer and Schaudinn (1918) by Muzaffar and Jones (2004) for *T. erostris* in *C. grylle* and *T. cylindraceus* in *Uria* spp. do not refer to independent field collections. Lastly, a record of *T. macrocephalus* in *U. aalge* attributed to von Linstow (1878) and Yamaguti (1959) cannot be validated.

Historical records, with provenance minimally based on field collections and published reports, for species of *Tetrabothrius* in alcid and larid seabirds are focused in the eastern North Atlantic/Russian Arctic, Greenland/northeastern Canada, and western North Pacific/Russian Far East (Table 3). In the greater North Atlantic basin and Russian Arctic: (1) *Tetrabothrius jagerskioeldi* (including *T. intrepidus*) was initially recognized and described based on multiple cestode specimens in black guillemot from Sweden and the Barents Sea, Russia (Nybelin, 1916; Baylis, 1918). (2) Markov (1937, 1941) did not reveal *T. jagerskioeldi* or other *Tetrabothrius* in 52 *U. lomvia* and 7 *C. grylle* at Bezymiannaya Bay, Novaya Zemlya; *T. cylindraceus* occurred in 33% of 17 *L. glaucous* but not in *Rissa tridactyla* (21). (3) Belopol'skaia (1952) based on field collection in 1940–41 reported *T. jagerskioeldi* in black guillemot (4.5% of 27 adults and 20% of 5 juveniles, 1–2 intensity); *Alca torda* (9.2% of 22, 1); *Uria aalge* (4% of 54 adults, 1); Atlantic puffin, *Fratercula arctica* (4.8% of 26 adults, 1); and *Stercorarius parasiticus* (21% of 30 adults, 3; 50% of 6 juveniles, 1) at the Seven Islands, Gosudarstvennogo Zapovednik in the Barents Sea. Specimens of *T. jagerskioeldi* were not observed or collected in black-legged kittiwakes, *Rissa tridactyla* (90 examined); great black-backed gull, *Larus marinus* Linnaeus (24); *Larus argentatus* (34), or *Larus canus* Linnaeus (31), although *T. erostris* and *T. cylindraceus* were revealed in these larids at this locality. (4) Galaktionov (1995) explored parasite diversity during 1991–93 in the Seven Islands Reserve and did not demonstrate *T. jagerskioeldi* or other species of *Tetrabothrius* among *C. grylle* (5 examined), *U. aalge* (10), *U. lomvia* (10), *F. arctica* (10), and *A. torda* (9). Among larids, *T. erostris* and *T. immerinus* (Abildgaard, 1790) were observed in black-legged kittiwakes, whereas herring gulls were infected with *T. erostris*; prevalence of *T. erostris* was substantially greater, and *T. cylindraceus* was not observed compared to data from the 1940s. (5) Galkin et al. (1994) examined 4 black guillemots and 6 thick-billed murres from Hooker Island (Franz Josef Land) and Kharlov Island (East Murman Coast) (Arctic) without observing *T. jagerskioeldi*; *T erostris*, *T. immerinus*, and *T. morschtini* were reported in 4 species of *Larus* gulls and black legged kittiwakes. (6) Kuklin and Kuklina (1995) reported *T. jagerskioeldi* in a black guillemot but not in other alcid hosts from the region of the Kola Peninsula based on collections between 1993 and 2000.

In Greenland/northeastern Canada: (1) Ditlevsen (1914) reported *T. cylindraceus* in thick-billed murre and *T. erostris* in black guillemot from unspecified localities in Greenland; (2) Baer (1956) reported *T. jagerskioeldi* in black guillemot from Kangerluk (= Diskofjord), West Greenland (determined to represent an undescribed species in the present study), and razorbill from Oqaitsoq, West Greenland (redetermined as *T. erostris* in current study) but not thick-billed murres; other species, *T. erostris* or *T. cylindraceus*, were reported in larids including glaucous gull, *Larus hyperboreus*, Iceland gull, *Larus glaucoides* Meyer, *Rissa tridactyla*, and Arctic tern, *Sterna paradise*, from West Greenland. (3) *Tetrabothrius jagerskioeldi* was not reported from Iceland by Baer (1962), and species of *Tetrabothrius* were not observed in razorbills, common puffins, and a single museum specimen of the now extinct great auk (*Pinguinus impennis* (Linnaeus)); other tetrabothriids included *T. cylindraceus* in *Rissa tridactyla*, *L. fuscus*, and *L. hyperboreus*, and *T. erostris* in *S. parasiticus* and *L. hyperboreus*. (4) Threlfall (1971) found *T. jagerskioeldi* in common murres (7% of 674, 1–19), thick-billed murres (8% of 60, 1–4) Atlantic puffin (2.5% of 160, 1), and possibly dovekie, *Alle alle* (Linnaeus), (4% of 48) across 6 geographic localities from the Northwest Atlantic, encompassing Newfoundland, Labrador, and western Greenland; also *T. cylindraceus* and *T. erostris* were found in *U. aalge* (near 1%). Razorbills and black guillemots were not demonstrated as hosts for species of *Tetrabothrius* in these collections. (5) Muzaffar (2009) examined common (43) and thick-billed murres (57) from 5 sites spanning Coats Island, Nunavut to Labrador and West Greenland and did not reveal *T. jagerskioeldi*, in contrast to occurrences reported by Threlfall (1971) 40 years earlier; an unidentified species of *Tetrabothrius* was found in a thick-billed murre.

In the western North Pacific: (1) Krotov and Deliamure (1952) reported *T. macrocephalus* in marbled murrelets, *Brachyramphus marmoratus*, from Sakhalin Island (ca. 51°N, 143°E); *Tetrabothrius jagerskioeldi* was not observed. (2) Belopol'skaia (1963a, 1963b) found *T. jagerskioeldi* in spectacled guillemots, and ancient murrelets from the Sudzukhinsky Reserve, Russian Far East. *Tetrabothrius jagerskioeldi* was not recognized in 7 species of Laridae, all of which had mixed-species infections of

T. erostris and *T. cylindraceus*. (3) Smetanina (1979, 1981) reported *T. jagerskioeldi* as a common parasite in alcid hosts during the period of colonial nesting and post-breeding at Peter the Great Bay, adjacent to Vladivostok (42°40′N, 132°00′E). Reports included cestodes in the following alcids: 5 spectacled guillemots (11.6% of 43 examined, intensity = 1–6); 2 thick-billed murres, *Uria lomvia*, (28% of 7, 1–11); and 1 ancient murrelet, *Synthliboramphus antiquus* (17% of 6, 6). These cestodes were not reported in other alcids: rhinoceros auklet, *Cerorhinca monocerata* (5 examined); *Uria aalge* (2); and least auklet, *Aethia pusilla* (8). Further, species of Laridae were not reported as hosts for *T. jagerskioeldi* although both *T. cylindraceus* and *T. erostris* were commonly observed among black-tailed gull, *Larus crassirostris* Vieillot (115 examined); herring gull, *Larus argentatus* (4); common gull, *Larus canus* (41); and 4 species of terns. (4) Smetanina and Leonov (1984) reported *T. jagerskioeldi* in rhinoceros auklet from Shikhotan Island, Kurile Islands (43°48′N, 146°45′E).

A conclusion that emerges is that *T. jagerskioeldi* is a rare tapeworm with a patchy distribution in pelagic to nearshore marine environments, showing considerable heterogeneity, with respect to prevalence and abundance, in space and time, among alcid seabirds across high-latitude seas of the Holarctic (e.g., Table 3; Supplementary Data Table 2). Prior concepts for host range in the current slice of ecological time require reevaluation. We demonstrate that the associations for *T. jagerskioeldi* are relatively narrow and appear to involve a more limited spectrum of alcid hosts, particularly guillemots, and less often other species of marine birds than currently assumed.

The apparent spatial patchiness for occurrence of *T. jagerskioeldi* and *Tetrabothrius* undescribed n. sp. among alcids contrasts with the distribution of other species of *Tetrabothrius* in larid hosts (Supplementary Data Table 2). Among species assemblages in sympatry involving alcids and larids, *T. jagerskioeldi* and *Tetrabothrius* undescribed n. sp. are rarely observed occurring in 1–7.5% of hosts. In contrast, prevalence of other *Tetrabothrius* spp. in species of larids may approach 80–100% adjacent to some colony sites. Species diversity for *Tetrabothrius* in alcids and larids generally represent distinct faunas with minimal overlap that may be ecologically defined (e.g., Hoberg, 1992; Supplementary Data Table 2). These apparent differences are unlikely to be an artifact of sampling. The outlines of diversity and parasite distribution in these marine systems reflect the outcomes of ecological fitting in sloppy fitness space, interactions of opportunity for exposure and transmission determined by physical and biological oceanographic processes, and capacity of parasites to utilize host resources among alcid and larid seabirds (e.g., Hoberg and Brooks, 2008; Agosta et al., 2010; Brooks et al., 2019). Further, a sympatric assemblage of avian species is not required for transmission, as the influence of advective processes downstream and across insular systems may influence the distribution and availability of suitable and infected intermediate hosts in the water column, either limiting or expanding opportunity (e.g., Hoberg, 1995). These are dynamic systems where oscillations in temperature, water masses, production cycles, and cascades emanating from incremental climate warming and extreme events are predicted to be reflected in faunal structure for parasites (Hoberg et al., 2013, 2017).

Faunal disparity is real with respect to parasite species diversity, prevalence, and intensity and reflects the distribution and density of seabirds, macrozooplankton, other marine invertebrates, and piscine prey in nearshore and neritic habitats versus pelagic environments (Hoberg, 1996, 2005). That tetrabothriids are in circulation in common marine food webs, however, is indicated by the abundance of those species among larid hosts (high prevalence). Density and dilution in marine environments are expected to influence the distribution and availability of prey species involved in parasite transmission with respect to islands and insular systems that serve as a focus for avian activity during the breeding cycle (e.g., Hoberg, 1996). Predictable currents, advective processes, and frontal eddy systems associated with islands and archipelagos focus the distribution of pelagic prey species and secondarily directly influence patterns of foraging activity for seabirds and other vertebrate hosts (e.g., Hoberg, 1995, 1996; Hoberg and Adams, 2000).

Necessity and Adequacy of Baselines for Diversity

Baselines, against which to assess environmental stability and perturbation, are only as good as the accuracy of the species identifications, the depth of associated biodiversity informatics, the holistic approach to community-level collections (Schindel and Cook, 2018, Galbreath et al., 2019), and authoritative archived specimens (with integrated data) that describe an ecological assemblage in space and time (e.g., Brooks et al., 2014; Cook et al., 2016; Dunnum, 2017). Diversity (species richness, abundance, host and geographic distributions) must be explored across an entire local or regional avifauna rather

than with a focus on specific putative host species. Evolution of diagnostic methods continues to expand, with increasingly refined molecular-based data that can contribute to accurate definitions of species limits and diversity in a phylogenetic/historical context (e.g., Brooks and McLennan, 2002; Cook et al., 2013, 2017; Colella et al., 2019; Greiman et al., 2018); integration of comparative morphology and molecular data remain a powerful foundation, although the latter could not be explored in our current study. Significantly, assumptions about host range linked to concepts of specificity are no longer supportable (e.g., Hoberg and Brooks, 2008; Nylin et al., 2018; Brooks et al., 2019). Our understanding of environmental drivers and episodic perturbation in host colonization, parasite diversification, and mosaic faunal assembly indicate that whole-ecosystem approaches are not only warranted but a necessity in identifying the outcomes of accelerating disruption of the biosphere (Brooks and Hoberg, 2000; Hoberg and Brooks, 2008; Hoberg et al., 2012; Brooks et al., 2019). Disruption modifies faunal structure through elimination of ecological constraints and by facilitating opportunities for colonization and expansion of host range that emerge from ecological fitting in sloppy fitness space (Agosta et al., 2010; Araujo et al., 2015; Hoberg and Brooks, 2015). The parameters for faunal dynamics, assembly, and diversity as identified in the *Stockholm Paradigm* and the *DAMA* protocols provide a path to anticipate and identify the outcomes of accelerating change, ecological perturbation, the nature of parasite-host systems, and potential for emerging disease in marine environments (Brooks et al., 2014; Brooks et al., 2019).

A robust understanding of parasite species diversity and distribution is critical in establishing baselines across marine ecosystems. Our current study among species of *Tetrabothrius*, especially in the North Pacific basin and Bering Sea ecosystem contributes to development of a specimen-centered series of baselines derived primarily from the late 1970s through the 1980s against which accelerating perturbations may be explored (e.g., broader assessments of helminth diversity in Hoberg, 1984; Hoberg et al., 2013). The 1970s represent a tipping point and a shift to accelerated warming that has been especially manifested in Arctic and northern ecosystems (Trenberth et al., 2007; reviewed in Hoberg et al., 2017). Thus, defining the limits for *T. jagerskioeldi*, other species of *Tetrabothrius*, and a broader macroparasite fauna has implications for understanding host range, geographic/oceanographic distributions, and the physical and biological determinants of faunal structure and assembly across evolutionary and ecological time (e.g., Galaktionov, 1995; Hoberg, 1996; Hoberg and Brooks, 2008; Cook et al., 2017; Brooks et al., 2014; Brooks et al, 2019).

Large-scale historical baselines established from specimen collections allow exploration of faunal change over time in neritic and pelagic systems (Hoberg and Adams, 2000; Hoberg, 2005), but parasites have not been regularly sampled and archived from North Pacific seabirds over the past three decades. Parasites become powerful adjuncts to studies of food habits and foraging ecology among diverse assemblages of hosts (Galaktionov, 1995; Hoberg et al., 2013). For example, Muzaffar (2009) observed a major shift in the distribution of *Tetrabothrius* occurring in common and thick-billed murres from West Greenland relative to intensive surveys in the late 1960s. In this regard, Threlfall (1971) had provided a baseline for comparison, reporting *T. jagerskioeldi* as an abundant cestode across multiple geographic sites and species of alcids; large *Tetrabothrius* in murres were considered to be absent 40 years later. Galaktionov (1995) also observed a substantial change in diversity and distribution for tetrabothriid faunas circulating in alcids and larids in the Seven Islands Archipelago, which was the site of inventory by Belopol'skaia (1952) in the 1940s. New patterns for host range and distribution were attributed to changing diets reflecting abundance of forage fishes: (1) absence of *T. jagerskioeldi* in alcid seabirds; (2) increasing abundance of *T. erostris* and absence of *T. cylindraceus* in *Larus* gulls; (3) first occurrence of *T. immerinus* (= *T. macrocepahlus*) and an undescribed species of *Tetrabothrius* in *Rissa tridactyla* (Galaktionov et. al., 1993; Galkin et al., 1994). Additionally, increasing prevalence of other cestodes, *Alcataenia larina* (Krabbe, 1869) in kittiwakes resulted from prey selection dominated by macrozooplankton including euphausiids and copepods. Considerable perturbation in the structure of host-parasite assemblages in Arctic and subarctic seas appear increasingly driven by climate forcing and variation in oceanographic conditions, current regimes, and range shifts. Shifting abundance of non-tetrabothriid cestodes appears related to differential prey selection (euphausiids) among kittiwakes and murres and oceanic regime shifts emerging from the Pacific Decadal Oscillation (Hoberg, 1996, 2005). Intensified current regimes and changing watermass structure through the Arctic basin were identified as drivers in an apparent range expansion from the North Pacific to the North Atlantic of a species of *Alcataenia* Spasskaya, 1971 in murres (Muzaffar et al., 2005; Muzaffar, 2009). Oceanic

colonization was apparently mediated by advection and an expanding range for euphausiid crustaceans of North Pacific origin that serve as intermediate hosts. Emerging host and geographic associations for parasites have coincided with a substantial restructuring of open ocean, pelagic habitats since the 1970s.

A series of mortality events among different species of seabirds (alcids, larids, and procellariiforms) has been documented across the Northeastern Pacific (Gulf of Alaska) and into the Bering Sea over the past 2–3 decades (reviewed in Jones et al., 2019). A broad scale and ongoing shift in ecosystem structure has been linked to recurring episodes of elevated sea surface temperatures at high latitudes (Jones et al., 2019; IPCC, 2019). Signatures of oceanic warming are apparent across scales and involve: (1) outcomes of incremental climate warming over time; (2) episodic oscillations between warm and cold ocean regimes defined by such ocean-atmosphere processes as El Niño Southern Oscillation and the Pacific Decadal Oscillation (Chavez et al., 2003; Springer et al., 2007; Sydeman et al., 2015); and (3) transient and spatially persistent events of extreme atmospheric and sea surface temperatures manifested as marine heat waves (Di Lorenzo et al., 2016; reviewed in Jones et al., 2018, 2019). A decreasing extent and duration of seasonal sea ice has resulted in elevated sea surface temperatures across the Bering Sea (and Arctic Basin) and is linked to ecological cascades influencing the distribution and diversity of forage fishes and zooplankton (Post et al., 2013; Duffy-Andersen et al., 2017; Perovich et al., 2017, 2018). Shifts in ecosystem structure appear to involve the community composition of lipid-rich macrozooplankton (euphausiids—species of *Thysanoessa* Brandt and calanoid copepods—species of *Neocalanus* Sars and *Calanus* Leach) and forage fishes (capelin—*Mallotus villosus* (Müller), juvenile Alaska Pollock—*Gadus chalcogrammus* Pallas, and possibly Pacific sandlance—*Ammodytes hexapterus* Pallas) that serve as primary prey for alcids and other seabirds (e.g., Springer et al., 2007; see also Galaktionov, 1995 for discussion of helminth faunas and ecological dynamics for fishes and zooplankton in the Barents Sea).

Perturbations in ecosystem structure and dynamics are manifested in mortality events for zooplanktivorous and piscivorous seabirds through modified phenology for prey, shifts in abundance, and altered patterns of diversity that influence the availability of suitable food resources (e.g., Baduini et al., 2001; Napp and Hunt, 2001; Jones et al., 2019). The greatest sustained or persistent marine heat wave documented to date for the Gulf of Alaska and Bering Sea, during 2016-2017, resulted in extensive breeding failures and an estimated mortality event for over 1 million common murres which represent the dominant marine avian piscivores in these oceanic systems (Piatt et al., 2020). Contemporary conditions in the Bering Sea ecosystem suggest northward shifts in the distribution of primary forage fishes and macrozooplankton tracking a reduction in the range of cold water and low sea surface temperatures. Availability of historically dominant assemblages of prey species is changing in a downstream response to elevated sea surface temperatures. Disruption of trophic pathways and connectivity across the greater North Pacific is expected to result in substantial changes in the distribution and abundance of a broad array of parasites that historically have circulated respectively among assemblages of marine birds, pinnipeds and cetaceans (e.g., Hoberg et al., 2013; Brooks et al., 2019).

In an increasingly variable regime, stratification by temperature/salinity in the water column, changing water mass structure, and new current patterns, and connectivity will modify the distribution and availability of primary zooplankton and piscine prey that serve as intermediate hosts. Secondarily, a shifting spectrum for prey diversity, spatially and temporally, will influence transmission dynamics, occurrence, and abundance for a range of helminth and other parasites in marine birds (Hoberg, 1996, 2005; Mouritsen and Poulin, 2002; Muzaffar et al., 2005; Muzaffar, 2009; Hoberg et al., 2013, 2017). Anthropogenic disturbance related to fisheries and other factors will also directly influence the structure and diversity of helminth communities, especially among larids (e.g., Galaktionov, 1995; Galaktionov et al., 1993). Beyond direct mortality events related to starvation, stress, and toxic algal blooms (Jones et al., 2019), we would predict substantial changes in the distribution of characteristic assemblages of macroparasites (and other pathogens) associated with species of seabirds and a diverse assemblage of vertebrates and invertebrates (e.g., Galaktionov, 1995; Hoberg, 1996, 2005; Hoberg et al., 2013, 2017). Acquisition of a macroparasite fauna in avian hosts results from extended bouts of foraging in space and time, reflecting seasonal and finer scale interactions across neritic to pelagic environments. Detailed knowledge of specimen-based faunal diversity for parasites provides access to a cumulative snapshot of foraging behavior, prey availability, and prey selection.

Interconnected and comparative snapshots can be assembled only through rigorous, temporally structured, resampling efforts that will provide powerful temporal and spatial perspectives and proxies for changing conditions in marine foodwebs, communities, and the continuity of trophic linkages (Hoberg et al., 2013). In the intervening decades since the core of this North Pacific inventory was assembled and archived, pervasive perturbations have been observed across the North Pacific and Bering Sea ecosystem. On expansive spatial and temporal scales the signatures for long-term incremental warming, decadal and short-term ocean-atmosphere oscillations, and emergence of extreme events are immediately apparent (Hoberg et al., 2017). Ongoing shifts in the structure of marine systems in response to temperature regimes are expected to drive changes in the diversity and distribution of assemblages of hosts and parasites with implications yet to be revealed and which are incompletely understood.

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Supplementary data tables follow.

Supplementary Data Table 1. Field Data with Geo-Referencing, Dates, and Collectors for Specimens of Alcidae, Some Laridae, and Other Seabirds Examined for Helminth Parasites from the Greater North Pacific Basin (1949–1992)

Aleutian Islands, Alaska

• Amchitka Island, Constantine Harbor, Rat Islands, Bering Sea (ca. 59°30′N, 179°00′E)
March 1952 / R. L. Rausch
May 1976 / E. P. Hoberg

• Alaid Island, Semichi Islands, Bering Sea (52°45′46″N, 173°53′53″E)
August 1992 / D. Siegel-Causey

• Attu Island (Holtz Bay), Near Islands, Bering Sea (52°56′50″N, 173°11′31″E)
July 1991, August 1992 / D. Siegel-Causey

• Attu Island (Etienne Bay), Near Islands, Bering Sea (52°53′53″N, 172°34′56″E)
August 1992 / D. Siegel-Causey

• Buldir Island, Bering Sea (ca. 52°21′N, 175°56′E)
July 1974 / C. P. Dau, G. V. Byrd, M. H. Dick
August 1975 / E. P. Hoberg
July 1982 / D. Forsell
August 1987 / D. Nysewander
August 1991 / D. Siegel-Causey

• Kiska Island, Kiska Harbor, Bering Sea (51°58′01″N, 177°33′50″E)
August 1992 / D. Siegel-Causey

• Niztki Island (Bozo Cove), Semichi Islands (52°44′28″N, 173°59′08″E)
August 1991 / D. Siegel-Causey

• South of Western Aleutian Islands, Pelagic Habitat, North Pacific (ca. 50–51°N, 172–174°E)
June–July 1981 / P. J. Gearin
14 July 1981 / P. J. Gearin (50°03′N, 173°08.6′E)
June 1982/ P. J. Gearin

Arctic Basin and Chukchi Sea

• Little Diomede Island, Bering Strait (65°45′42″N, 168°57′06″W)
15 August 1984 / L. Lowry

• Point Barrow, Alaska, Chukchi Sea (71°16′N, 156°50′N)
May 1958 / R. L. Rausch
August 1979 / J. Homan

• Cape Thompson, Alaska, Chukchi Sea (ca. 68°06′N, 165°46′W)
June 1959 / L. G. Swartz
June 1960 / L. G. Swartz
July 1976 / D. G. Roseneau, A. M. Springer
July 1977 / D. G. Roseneau, A. M. Springer

• Cape Lisburne, Alaska, Chukchi Sea (ca. 68°52′N, 166°12′W)
July 1977 / D. G. Roseneau, A. M. Springer

• Chaun Bay (Chaun Biological Station), East Siberian Sea, Russia (ca. 68°44′N, 170°36′E)
July–August 1981 / V. Kontrimavichus, S. Bondarenko, A. Ia. Kondratiev, L. Kondratieva, G. Atrashkevich, E. P. Hoberg

Bering Sea

• St. Paul Island (Pribilof Islands), Bering Sea (57°10′N, 170°20′W)
July 1979 / J. Homan
June 1987 / G. V. Byrd

• St. George Island (Pribilof Islands), Bering Sea (56°36′00″N, 169°32′00″W)
June 1987 / G. V. Byrd

• Pribilof Islands, Pelagic (no specific geo coordinates)
August 1974 / US Fish and Wildlife Service

• Nunivak Island, Nash Harbor, Bering Sea (66°00′N, 166°00′W)
August 1949 / P. J. Brandly

• St. Matthew Island, Bering Sea (ca. 60°20′N, 171°00′W)
July–August 1982 / E. P. Hoberg, M. Dykes-Hoberg, M. K. Hoberg, D. G. Roseneau
July 1983 / A. M. Springer

• St. Lawrence Island, Bering Sea (ca. 63°45′N, 171°40′W)
May 1950 / E. L. Schiller
18 August 1950 / E. L. Schiller / (63°40′04″N, 170°34′08″W)
22 August 1950 / E. L. Schiller / (Gambell) (63°46′48″N, 171°44′25″W)
5 August 1956 / F. H. Fay / Boxer Bay (63°20′21″N, 171°34′25″W)
July 1959 / R. L. Rausch
August 1964 / J. Bédard / (Gambell) (63°46′48″N, 171°44′25″W)
10 and 27 July 1966 / J. Bédard / (Gambell) (63°46′48″N, 171°44′25″W)
August 1966 / J. Bédard / (Gambell) (63°46′48″N, 171°44′25″W)
August 1968 / J. Bédard / (Gambell) (63°46′48″N, 171°44′25″W)
30–31 May, June 1981 / R. Wilson / (Savoonga) (63°41′48″N, 170°27′39″W)
19 July 1981 / D. G. Roseneau, A. Springer / (Savoonga) (63°41′48″N, 170°27′39″W)
June 1982 / R. L. Rausch / (Savoonga) (63°41′48″N, 170°27′39″W)
June 1983 / R. L. Rausch
18 June 1987 / J. Piatt

• Sledge Island, Bering Sea (64°29′45″N, 166°12′08″W)
July 1969 / R. L. Rausch

• Wales, Alaska, Bering Sea (65°36′N, 168°05′W)
22 March 1966 / R. L. Rausch

• Bering Sea, North Central (no specific coordinates)
1976, 1977 / US Fish and Wildlife Service

Gulf of Alaska

• Ugaiushak Island, Gulf of Alaska (56°47′N, 156°41′W)
May–July 1976 / E. P. Hoberg, D. H. S. Wehle

• Central Island, Gulf of Alaska (56°51′N, 156°53′W)
June 1976 / E. P. Hoberg, D. H. S. Wehle

• Chowiet Island, Semidi Islands, Gulf of Alaska (ca. 56°02′N, 156°45′W)
June 1976 / G. C. Burrell

• Big Koniuji Island, Shumagin Islands, Gulf of Alaska (ca. 55°03′N, 159°35′W)
July 1976 / US Fish and Wildlife Service

• Kodiak Island, Uganik Bay, Gulf of Alaska (57°47′21″N, 153°31′47″W)
June 1953 / R. L. Rausch

• Kodiak Island, Uyak Bay, Browns Lagoon, Gulf of Alaska (57°42′52″N, 153°56′51″W)
June 1953 / R. L. Rausch

• Kodiak Island, Chiniak Bay, Gulf of Alaska (57°49′N, 152°30′W)
June–July 1977 / E. P. Hoberg, D. Nysewander

• Puffin Island, Kodiak Island, Chiniak Bay, Gulf of Alaska (57°46′N, 152°26′W)
10 July 1977 / E. P. Hoberg
24 July 1977 / E. P. Hoberg

• Sitkalidik Island, Kodiak Island region, Gulf of Alaska (57°07′N, 153°10′W)
8 July 1977 / P. Baird, A. Moe

• Middleton Island, Gulf of Alaska (59°29′N, 146°28′W)
June 1956 / R. L. Rausch
November 1956 / R. L. Rausch

• Shuyak Island, Big Bay, Gulf of Alaska (58°33′23″N, 152°36′14″W)
November 1954 / R. L. Rausch

• Forrester Island, Gulf of Alaska (54°50′N, 133°35′W)
July 1976 / A. DeGange

• Gulf of Alaska, North Central (no specific geo coordinates)
1969, 1970, 1971 / US Fish and Wildlife Service

Eastern North Pacific/Washington State to California

Washington State, USA

• Grays Marine Canyon (Washington pelagic zone) (46°55′N, 124°46′W)
8 September 1982 / E. P. Hoberg, D. R. Paulson, K. B. Aubry
31 August 1985 / E. P. Hoberg, S. Rowher, K. B. Aubry, C. Spaa
21 September 1985 / E. P. Hoberg, G. Eddy, S. Rowher
21 August 1987 / E. P. Hoberg, S. Rowher, K. B. Aubry

• Protection Island, Strait of Juan de Fuca (48°08′N, 122°55′W)
July 1981 / R. Fitzner

• Destruction Island, Washington, Eastern North Pacific (47°41′N, 122°55′W)
July 1981 / R. Fitzner

• San Juan Island, Friday Harbor, Washington (48°32′7″N, 123°1′52″W)
January 1981 / E. P. Hoberg

• San Juan Island, Wescott Bay, Washington (ca. 48°30′N, 123°05′W)
February 1982 / W. G. English

• Pt. Roberts (Southern Strait of Georgia [49°00′N, 123°05′W])
January 1964 / R. A. Ryder

• Sequim Bay, Olympic Peninsula, Strait of Juan de Fuca (ca. 48°05′N, 123°00′W)
November 1981 / E. P. Hoberg, R. Fitzner

California, USA

• Humboldt Bay, Eastern North Pacific (ca. 40°49′N, 124°10′W)
June 1977 and 1979 / M. Phillips

• Santa Barbara Island (Channel Islands), Eastern North Pacific (ca. 33°28′30″N, 119°02′13″W)
10 June 1987 / C. Drost
12 May 1988 / C. Drost

Sea of Okhotsk, Russia

• Magadan, coastal zone (ca. 59°35′N, 150°45′E)
August 1981 / A. Ia. Kondratiev

• Khmotiyevskogo Peninsula (near Talan Island), northern Sea of Okhotsk (ca. 59°18′N, 148°56′E)
30 July 1988 / L. Kondratieva

• Talan Island Northern Sea of Okhotsk (ca. 59°19′N, 149°06′E)
July 1988 / E. P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko
September 1988

Supplementary Data Table 2. Geography, Hosts, and Species of *Tetrabothrius* from the Greater North Pacific Basin

Region	Geographic Location	Collection Date	Avian Species	*N* = Examined	*TETRABOTHRIUS* SPECIES INFECTION								
					Tetrabothrius jagerskioeldi			*Tetrabothrius* n. sp. Undescribed			*Tetrabothrius* spp.		
					N =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)
Gulf of Alaska	Ugaiushak Island	May–July 1976	*Uria aalge*	31	0	0–0		0	0–0		0	0–0	
			Uria lomvia	19	0	0–0		1	5		0	0–0	
			Cepphus columba	1	1	1	MSB PARA 27928	0	0–0		0	0–0	
			Cerorhinca monocerata	2	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata	30	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata	10	0	0–0		1	1		0	0–0	
			Rissa tridactyla	35	0	0–0		0	0–0		18	1–5	
	Central Island (Ugaiushak Island Region)	June 1976	*Larus glaucescens*	20	4	1–4	MSB PARA 27873, 27874, 27872, 27871	0	0–0		20	3–18	
	Middleton Island	November 1956	*Uria aalge*	1	0	0–0		0	0–0		0	0–0	
		June 1956	*Rissa tridactyla*	1	0	0–0		0	0–0		1	1	
			Larus glaucescens	1	0	0–0		0	0–0		1	1	
	Shuyak Island	November 1954	*Uria aalge*	1	1	1	MSB PARA 5732	0	0–0		0	0–0	
	Semidi Islands	June 1976	*Uria aalge*	2	0	0–0		0	0–0		0	0–0	
			Uria lomvia	3	0	0–0		0	0–0		0	0–0	
	Forrester Island	July 1976	*Cerorhinca monocerata*	2	0	0–0		0	0–0		0	0–0	
			Ptychoramphus aleuticus	1	0	0–0		0	0–0		0	0–0	
			Synthliboramphus antiquus	1	0	0–0		0	0–0		0	0–0	
	Kodiak Island (Chiniak Bay)	June–July 1977	*Uria aalge*	14	0	0–0		0	0–0		0	0–0	
			Uria aalge (subadult)	20	0	0–0		5	1–4		4	1–3	
			Uria aalge (fledgling)	1	0	0–0		0	0–0		0	0–0	
			Uria lomvia	1	0	0–0		0	0–0		0	0–0	
			Brachyramphus brevirostris	3	0	0–0		0	0–0		0	0–0	
			Brachyramphus marmoratus	3	1	9	MSB PARA 27916	0	0–0		0	0–0	
			Synthliboramphus antiquus	1	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata	72	0	0–0		0	0–0		6	1–10	
			Fratercula corniculata	19	0	0–0		1	1		1	1	
			Rissa tridactyla	50	0	0–0		0	0–0		22	1–8	
			Larus glaucescens	11	0	0–0		0	0–0		10	1–33	
	Puffin Island (Kodiak Island Region)	July 1977	*Larus glaucescens*	20	10	1–6	MSB PARA 27876, 27886, 27894, 27902, 27883, 27905, 27908, 27898, 27875, 27890	0	0–0		19	1–38	
	Kodiak Island (Uganik Bay)	May 1953	*Cepphus columba*	1	1	5	MSB PARA 3990	0	0–0		0	0–0	
	Kodiak Island (Uyak Bay)	June 1953	*Cepphus columba*	1	1	1	MSB PARA 4046	0	0–0		0	0–0	
	Sitkalidik Island (Kodiak Island Region)	July 1977	*Fratercula cirrhata*	5	0	0–0		0	0–0		1	1	
			Rissa tridactyla	5	0	0–0		0	0–0		2	1–4	
	Big Koniuji Island	July 1976	*Aethia psittacula*	1	0	0–0		0	0–0		0	0–0	

Supplementary Data Table 2. Geography, Hosts, and Species of *Tetrabothrius* from the Greater North Pacific Basin

Region	Geographic Location	Collection Date	Avian Species	*N* = Examined	*TETRABOTHRIUS* SPECIES INFECTION								
					Tetrabothrius jagerskioeldi			*Tetrabothrius* n. sp. Undescribed			*Tetrabothrius* spp.		
					N =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)
	Gulf of Alaska – North Central	1969–1971	*Uria lomvia*	6	0	0–0		0	0–0		0	0–0	
Aleutian Islands	Amchitka Island	March 1952	*Brachyramphus marmoratus*	1	0	0–0		0	0–0		0	0–0	
			Aethia cristatella	2	0	0–0		1	1		0	0–0	
	Amchitka Island	May 1976	*Larus glaucescens*	13	0	0–0		0	0–0		4	1–2	
	Buldir Island	July 1974	*Cepphus columba*	1	0	0–0		0	0–0		0	0–0	
			Aethia psittacula	5	0	0–0		0	0–0		0	0–0	
			Aethia cristatella	1	0	0–0		0	0–0		0	0–0	
			Aethia pygmaea	3	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata	1	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata	2	0	0–0		0	0–0		2	1–8	
			Rissa brevirostris	1	0	0–0		0	0–0		1	6	
			Urile urile	1	0	0–0		0	0–0		0	0–0	
	Buldir Island	August 1975	*Uria lomvia*	11	0	0–0		1	1		0	0–0	
			Fratercula cirrhata	26	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata	13	0	0–0		2	1		1	1	
			Rissa tridactyla	10	0	0–0		0	0–0		9	1–14	
			Rissa brevirostris	1	0	0–0		0	0–0		0	0–0	
			Urile pelagicus	4	1	1	MSB PARA 27910	0	0–0		0	0–0	
			Urile urile	1	0	0–0		0	0–0		0	0–0	
	Buldir Island	July 1982	*Aethia pygmaea*	5	0	0–0		0	0–0		0	0–0	
	Buldir Island	August 1987	*Aethia pygmaea*	10	0	0–0		1	1		0	0–0	
			Aethia cristatella	8	0	0–0		0	0–0		0	0–0	
	Buldir Island	August 1991	*Urile pelagicus*	3	0	0–0		0	0–0		0	0–0	
	Nitzki Island (Bozo Cove)	August 1991	*Urile urile*	4	0	0–0		0	0–0		0	0–0	
	Attu Island (Holtz Bay)	July 1991	*Urile pelagicus*	2	0	0–0		0	0–0		0	0–0	
			Urile "kenyoni"	2	0	0–0		0	0–0		0	0–0	
	Attu Island (Holtz Bay)	August 1992	*Urile urile*	9	0	0–0		0	0–0		0	0–0	
	Attu Island (Etienne Bay)	August 1992	*Urile urile?*	10	0	0–0		0	0–0		0	0–0	
			Urile pelagicus	1	0	0–0		0	0–0		0	0–0	
	Alaid Island	August 1992	*Urile urile*	1	0	0–0		0	0–0		0	0–0	
			Urile pelagicus	5	0	0–0		0	0–0		0	0–0	
	Kiska Island (Kiska Harbor)	August 1992	*Urile pelagicus*	4	0	0–0		0	0–0		0	0–0	
	Western Aleutian (Pelagic)	June–July 1981, June 1982	*Uria lomvia* (subadult)	4	0	0–0		2	2–16		0	0–0	
			Synthliboramphus antiquus	1	0	0–0		1	1		0	0–0	
			Aethia cristatella	16	0	0–0		0	0–0		0	0–0	
			Cerorhinca monocerata	1	1	1	MSB PARA 26828	1	2		0	0–0	
			Fratercula cirrhata (adult)	30	0	0–0		6	1–5		3	1–5	
			Fratercula cirrhata (subadult)	23	0	0–0		2	1–2		0	0–0	
			Fratercula corniculata (adult)	12	0	0–0		2	1–8		0	0–0	
			Fratercula corniculata (subadult)	7	0	0–0		3	3–5		1	1	
Bering Sea	Wales, Alaska	March 1966	*Uria lomvia*	1	0	0–0		0	0–0		0	0–0	

Supplementary Data Table 2. Geography, Hosts, and Species of *Tetrabothrius* from the Greater North Pacific Basin

Region	Geographic Location	Collection Date	Avian Species	*N* = Examined	*TETRABOTHRIUS* SPECIES INFECTION								
					Tetrabothrius jagerskioeldi			*Tetrabothrius* n. sp. Undescribed			*Tetrabothrius* spp.		
					N =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)
	Sledge Island	**July 1969**	*Cepphus columba*	1	1	1	MSB PARA 27879	0	0–0		0	0–0	
	Nunivak Island (Nash Harbor)	**August 1949**	*Fratercula cirrhata*	2	0	0–0		0	0–0		0	0–0	
	Pribilof Islands – Pelagic	**August 1974**	*Uria lomvia*	1	0	0–0		0	0–0		0	0–0	
	St. Paul Island (Pribilof Islands)	**July 1979**	*Uria lomvia*	1	0	0–0		0	0–0		0	0–0	
			Aethia psittacula	2	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata	7	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata	7	0	0–0		0	0–0		0	0–0	
			Rissa tridactyla	10	0	0–0		0	0–0		0	0–0	
			Urile urile	3	0	0–0		0	0–0		0	0–0	
	St. Paul Island (Pribilof Islands)	**June 1987**	*Aethia cristatella*	1	0	0–0		1	1		0	0–0	
			Aethia pusilla	4	0	0–0		0	0–0		0	0–0	
			Aethia psittacula	5	0	0–0		0	0–0		0	0–0	
	St. George Island (Pribilof Islands)	**June 1987**	*Aethia cristatella*	8	0	0–0		0	0–0		0	0–0	
			Aethia pusilla	8	0	0–0		0	0–0		0	0–0	
			Aethia psittacula	2	0	0–0		0	0–0		0	0–0	
	St. Lawrence Island	**May 1950**	*Uria lomvia*	2	0	0–0		0	0–0		0	0–0	
			Larus hyperboreus	1	0	0–0		0	0–0		0	0–0	
	St. Lawrence Island (Gambell)	**August 1950**	*Cepphus columba*	4	2	1	MSB PARA 27880, 28951	1	1		0	0–0	
			Uria lomvia	1	0	0–0		1	1		0	0–0	
			Fratercula cirrhata	1	0	0–0		0	0–0		0	0–0	
			Rissa tridactyla	1	0	0–0		0	0–0		1	1	
	St. Lawrence Island	**August 1956**	*Cepphus grylle*	1	1	1	MSB PARA 1738	0	0–0		0	0–0	
	St. Lawrence Island	**July 1959**	*Urile pelagicus*	1	0	0–0		0	0–0		0	0–0	
	St. Lawrence Island	**August 1964**	*Aethia cristatella*	12	0	0–0		0	0–0		0	0–0	
			Aethia psittacula	1	0	0–0		0	0–0		0	0–0	
			Aethia pusilla	10	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata	1	0	0–0		0	0–0		0	0–0	
			Synthliboramphus antiquus	1	0	0–0		1	1		0	0–0	
			Fratercula corniculata	2	0	0–0		0	0–0		0	0–0	
			Uria aalge	1	0	0–0		0	0–0		0	0–0	
	St. Lawrence Island (Gambell)	**August 1966**	*Aethia cristatella*	2	0	0–0		0	0–0		0	0–0	
	St. Lawrence Island	**June 1968**	*Alle alle*	1	0	0–0		0	0–0		0	0–0	
	St. Lawrence Island (Savoonga)	**May–June–July 1981**	*Aethia cristatella*	6	0	0–0		0	0–0		0	0–0	
			Aethia pusilla	4	0	0–0		0	0–0		0	0–0	
			Aethia psittacula	2	0	0–0		1	1		0	0–0	
			Uria lomvia	2	0	0–0		1	5		0	0–0	
	St. Lawrence Island (Savoonga)	**June 1982**	*Aethia pusilla*	12	0	v		0	0–0		0	0–0	
	St Lawrence Island	**June 1983**	*Aethia psittacula*	1	0	0–0		0	0–0		0	0–0	

Supplementary Data Table 2. Geography, Hosts, and Species of *Tetrabothrius* from the Greater North Pacific Basin

Region	Geographic Location	Collection Date	Avian Species	*N* = Examined	*TETRABOTHRIUS* SPECIES INFECTION								
					Tetrabothrius jagerskioeldi			*Tetrabothrius* n. sp. Undescribed			*Tetrabothrius* spp.		
					N =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)
	St. Lawrence Island	June 1987	*Aethia cristatella*	10	0	0–0		0	0–0		0	0–0	
	St. Matthew Island	July 1982	*Aethia cristatella*	11	0	0–0		0	0–0		0	0–0	
			Aethia pusilla	24	0	0–0		1	1		0	0–0	
			Aethia psittacula	6	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata	5	0	0–0		0	0–0		0	0–0	
			Cepphus columba	11	2	1–2	MSB PARA 27927, 27919	1	1		0	0–0	
			Uria aalge (adult)	38	0	0–0		3	1		0	0–0	
			Uria aalge (subadult)	4	0	0–0		0	0–0		0	0–0	
			Uria lomvia (adult)	34	0	0–0		4	1-2		0	0–0	
			Uria lomvia (subadult)	3	0	0–0		2	1		0	0–0	
			Larus hyperboreus	1	0	0–0		0	0–0		1	1	
			Rissa tridactyla	14	0	0–0		0	0–0		2	1–2	
	St. Matthew Island	July 1983	*Uria aalge*	2	0	0–0		0	0–0		0	0–0	
			Uria lomvia	1	0	0–0		0	0–0		0	0–0	
	Bering Sea – North Central	1976–1977	*Uria aalge*	3	0	0–0		0	0–0		0	0–0	
			Uria lomvia	5	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata	5	0	0–0		0	0–0		0	0–0	
			Onychoprion aleutica	1	0	0–0		0	0–0		0	0–0	
Arctic Basin and Chukchi Sea	Barrow, Alaska	May 1958	*Uria aalge*	1	0	0–0		0	0–0		0	0–0	
	Barrow, Alaska	August 1979	*Cepphus grylle*	7	0	0–0		0	0-0		0	0–0	
			Rissa tridactyla	3	0	0–0		0	0–0		0	0–0	
			Larus hyperboreus	2	0	0–0		0	0–0		0	0–0	
			Stercorarius parasiticus	1	0	0–0		0	0–0		0	0–0	
			Sterna paradisaea	13	0	0–0		0	0–0		0	0–0	
			Xema sabini	11	0	0–0		0	0–0		0	0–0	
	Cape Thompson, Alaska	1959, 1960	*Uria lomvia*	29	0	0–0		6	?		0	0–0	
			Uria aalge	5	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata	8	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata	2	0	0–0		0	0–0		0	0–0	
			Rissa tridactyla	8	0	0–0		0	0–0		2	1–5	
	Cape Thompson, Alaska	July 1976	*Uria lomvia*	2	0	0–0		0	0–0		0	0–0	
			Uria aalge	1	0	0–0		0	0–0		1	1	
			Larus hyperboreus	1	0	0–0		0	0–0		0	0–0	
			Rissa tridactyla	2	0	0–0		0	0–0		0	0–0	
	Cape Thompson, Alaska	July 1977	*Uria lomvia*	16	0	0–0		0	0–0		0	0–0	
			Rissa tridactyla	1	0	0–0		0	0–0		0	0–0	
	Cape Lisburne, Alaska	July 1977	*Uria aalge*	1	0	0–0		1	1		0	0–0	
	Little Diomede Island, Alaska	July 1984	*Uria aalge*	4	0	0–0		0	0–0		0	0–0	
	Chaun Bay, Russia	July–August 1981	*Larus argentatus*	11	0	0–0		0	0–0		4	1+	
			Larus hyperboreus	8	0	0–0		0	0–0		2	1+	
			Xema sabini	2	0	0–0		0	0–0		0	0–0	
			Sterna paradisaea	23	0	0–0		0	0–0		0	0–0	
			Stercorarius longicaudus	2	0	0–0		0	0–0		0	0–0	
Sea of Okhotsk	Magadan, Russia	August 1981	*Uria aalge*	10	0	0–0		0	0–0		0	0–0	

Supplementary Data Table 2. Geography, Hosts, and Species of *Tetrabothrius* from the Greater North Pacific Basin

Region	Geographic Location	Collection Date	Avian Species	*N* = Examined	*TETRABOTHRIUS* SPECIES INFECTION								
					Tetrabothrius jagerskioeldi			*Tetrabothrius* n. sp. Undescribed			*Tetrabothrius* spp.		
					N =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)
			Fratercula cirrhata	5	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata	1	0	0–0		0	0–0		0	0–0	
			Rissa tridactyla	10	0	0–0		0	0–0		8	1–9	
			Larus schistisagus	1	0	0–0		0	0–0		1	1	
	Talan Island, Russia	**July–August 1988**	*Aethia cristatella* (adult)	80	0	0–0		5	1–3		0	0–0	
			Aethia cristatella (fledgling)	33	0	0–0		2	1		0	0–0	
			Aethia psittacula (adult)	27	0	0–0		2	1–3		0	0–0	
			Aethia psittacula (fledgling)	4	0	0–0		0	0–0		0	0–0	
			Synthliboramphus antiquus	46	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata (adult)	30	0	0–0		1	1		0	0–0	
			Fratercula cirrhata (fledgling)	33	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata (adult)	30	0	0–0		0	0–0		0	0–0	
			Fratercula corniculata (fledgling)	28	0	0–0		1	1		0	0–0	
			Uria aalge (adult)	29	0	0–0		1	4		0	0–0	
			Uria aalge (fledgling)	12	0	0–0		8	1–4		0	0–0	
			Uria lomvia (adult)	6	0	0–0		0	0–0		0	0–0	
			Uria lomvia (fledgling)	2	0	0–0		1	1		0	0–0	
			Rissa tridactyla (adult)	30	0	0–0		0	0–0		5	1–8	
			Rissa tridactyla (fledgling)	26	0	0–0		0	0–0		25	1–31	
			Larus schistisagus (adult)	21	0	0–0		0	0–0		14	1–34	
			Larus schistisagus (fledgling)	5	0	0–0		0	0–0		4	1–19	
			Urile pelagicus	3	0	0–0		0	0–0		0	0–0	
	Khmotiyevskogo Peninsula (near Talan Island, Russia)	**July 1988**	*Cepphus carbo*	4	2	1–3	MSB PARA 27912, 29234	0	0–0		1	3	
Eastern Pacific	**Grays Marine Canyon, Washington State, Pelagic Zone**	**September 1982**	*Ptychoramphus aleuticus*	4	0	0–0		1	1		1	1	
			Cerorhinca monocerata	1	0	0–0		0	0–0		0	0–0	
			Fratercula cirrhata	1	0	0–0		0	0–0		0	0–0	
			Xema sabini	2	0	0–0		0	0–0		0	0–0	
			Stercorarius pomarinus	1	0	0–0		0	0–0		0	0–0	
	Grays Marine Canyon	**August 1985**	*Brachyramphus marmoratus*	1	0	0–0		0	0–0		0	0–0	
			Cerorhinca monocerata	1	0	0–0		0	0–0		0	0–0	
			Larus heermani	6	0	0–0		0	0–0		2	1	
			Stercorarius pomarinus	6	0	0–0		0	0–0		0	0–0	
			Stercorarius longicaudus	2	0	0–0		0	0–0		0	0–0	
	Grays Marine Canyon	**September 1985**	*Ptychoramphus aleuticus*	10	0	0–0		6	1–2		0	0–0	
			Cerorhinca monocerata	3	0	0–0		2	1–4		0	0–0	
			Stercorarius parasiticus	2	0	0–0		0	0–0		0	0–0	
			Stercorarius pomarinus	6	0	0–0		0	0–0		1	1	
			Xema sabini	11	0	0–0		0	0–0		6	2–43	
			Larus argentatus	1	0	0–0		0	0–0		1	5	
	Grays Marine Canyon	**August 1987**	*Ptychoramphus aleuticus*	1	0	0–0		0	0–0		0	0–0	
			Cerorhinca monocerata	9	0	0–0		4	1		1	3	
			Fratercula cirrhata	11	0	0–0		0	0–0		0	0–0	
			Uria aalge (adult)	4	0	0–0		2	2–17		1	1	
			Uria aalge (subadult)	4	0	0–0		3	1–19		1	5	
			Stercorarius pomarinus	1	0	0–0		0	0–0		0	0–0	
			Stercorarius longicaudus	14	0	0–0		0	0–0		1	1	
			Stercorarius parasiticus	1	0	0–0		0	0–0		0	0–0	
			Sterna paradisaea	1	0	0–0		0	0–0		0	0–0	
			Xema sabini	8	0	0–0		0	0–0		5	1+	
	Pt. Roberts, Washington	**January 1964**	*Brachyramphus marmoratus*	1	0	0–0		0	0–0		1	3	

Supplementary Data Table 2. Geography, Hosts, and Species of *Tetrabothrius* from the Greater North Pacific Basin

Region	Geographic Location	Collection Date	Avian Species	*N* = Examined	*TETRABOTHRIUS* SPECIES INFECTION								
					Tetrabothrius jagerskioeldi			*Tetrabothrius* n. sp. Undescribed			*Tetrabothrius* spp.		
					N =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)	*N* =	Intensity Range	Museum Catalog Number(s)
	Protection Island, Washington	July 1981	*Cerorhinca monocerata*	10	0	0–0		0	0–0		0	0–0	
	Destruction Island, Washington	July 1981	*Cerorhinca monocerata*	10	0	0–0		1	4		0	0–0	
	Sequim Bay, Washington	November 1981	*Uria aalge*	20	0	0–0		0	0–0		0	0–0	
	San Juan Island, Friday Harbor, Washington	January 1981	*Brachyramphus marmoratus*	1	0	0–0		0	0–0		0	0–0	
	San Juan Island, Washington (Wescott Bay)	February 1982	*Cepphus columba*	2	0	0–0		0	0–0		0	0–0	
	Humboldt Bay, California	June 1977 and June 1979	*Uria aalge* (adult)	47	0	0–0		4	1–8		0	0–0	
			Uria aalge (fledgling)	18	0	0–0		3	2–14		0	0–0	
	Channel Islands, California (Santa Barbara Island)	June 1987	*Synthliboramphus scrippsi*	2	0	0–0		1	20		0	0–0	
	Channel Islands, California (Santa Barbara Island)	May 1988	*Synthliboramphus scrippsi*	2	0	0–0		0	0–0		0	0–0	
			Total	1826	29			102			218		

Supplementary Data Table 3. *Tetrabothrius jagerskioeldi* Nybelin, 1916 from North Pacific Localities with Museum of Southwestern Biology Catalogue Numbers (MSB PARA)

MSB PARA	Specimen Identifier	Specimen Collector(s)	Field Collection Number(s)	Geographic Locality of Collection	Geocoordinates of Collection	Date of Collection	Host Species
27910	Eric P. Hoberg	Eric P. Hoberg	EPH 30	Buldir Island, Aleutian Islands	52°22′59″N, 175°51′09″E	1975-08-14	*Urile pelagicus* (Pallas, 1811)
27873	Eric P. Hoberg	Eric P. Hoberg and Duff H. S. Wehle	EPH 145	Central Island (near Ugaiushak Island), Gulf of Alaska	56°51′N, 156°53′W	1976-07-09	*Larus glaucescens* Naumann, 1840
27874	Eric P. Hoberg	Eric P. Hoberg and Duff H. S. Wehle	EPH 146	Central Island (near Ugiaushak Island), Gulf of Alaska	56°51′N, 156°53′W	1976-07-09	*Larus glaucescens*
27872	Eric P. Hoberg	Eric P. Hoberg and Duff H. S. Wehle	EPH 144	Central Island, (near Ugaiushak Island), Gulf of Alaska	56°51′N, 156°53′W	1976-07-09	*Larus glaucescens*
27871	Eric P. Hoberg	Eric P. Hoberg and Duff H. S. Wehle	EPH 139	Central Island, (near Ugaiushak Island), Gulf of Alaska	56°51′N, 156°53′W	1976-07-09	*Larus glaucescens*
27912	Eric P. Hoberg	Luba Kondratieva	EPH 2622	Khmotiyevskogo Peninsula, Sea of Okhotsk	ca. 59°18′03″N, 148°56′10″E	1988-07-30	*Cepphus carbo* Pallas, 1811
29234	Eric P. Hoberg	Luba Kondratieva	EPH 2621	Khmotiyevskogo Peninsula, Sea of Okhotsk	ca. 59°18′03″N, 148°56′10″E	1988-07-30	*Cepphus carbo*
27916	Eric P. Hoberg	Eric P. Hoberg	EPH 264	Kodiak Island, Chiniak Bay, Gulf of Alaska	57°49′N, 152°30′W	1977-03-27	*Brachyramphus marmoratus* (Gmelin, 1789)
3990	Eric P. Hoberg	Robert L. Rausch	RLR 12739	Kodiak Island, Uganik Bay, Gulf of Alaska	57°47′21″N, 153°31′47″W	1953-05-08	*Cepphus columba* Pallas, 1811
4046	Eric P. Hoberg	Robert L. Rausch	RLR 12754	Kodiak Island, Uyak Bay, Browns Lagoon, Gulf of Alaska	57°42′52″N, 153°56′51″W	1953-06-11	*Cepphus columba*
27876	Eric P. Hoberg	Eric P. Hoberg	EPH 397	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-10	*Larus glaucescens*
27886	Eric P. Hoberg	Eric P. Hoberg	EPH 436	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-24	*Larus glaucescens*
27894	Eric P. Hoberg	Eric P. Hoberg	EPH 439	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-24	*Larus glaucescens*
27902	Eric P. Hoberg	Eric P. Hoberg	EPH 441	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-24	*Larus glaucescens*
27883	Eric P. Hoberg	Eric P. Hoberg	EPH 435	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-24	*Larus glaucescens*
27905	Eric P. Hoberg	Eric P. Hoberg	EPH 442	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-24	*Larus glaucescens*
27908	Eric P. Hoberg	Eric P. Hoberg	EPH 443	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-24	*Larus glaucescens*
27898	Eric P. Hoberg	Eric P. Hoberg	EPH 438	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-24	*Larus glaucescens*
27875	Eric P. Hoberg	Eric P. Hoberg	EPH 389	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-10	*Larus glaucescens*
27890	Eric P. Hoberg	Eric P. Hoberg	EPH 437	Puffin Island–Kodiak Island, Chiniak Bay, Gulf of Alaska	57°46′N, 152°26′W	1977-07-24	*Larus glaucescens*
27880	Eric P. Hoberg	Everett L. Schiller	RLR 8154, EPH 515	Gambell, Saint Lawrence Island, Bering Sea	63°40′04″N, 170°34′08″W	1950-08-18	*Cepphus columba*
28951	Eric P. Hoberg	Everett L. Schiller	RLR 8235, EPH 502	Gambell, Saint Lawrence Island, Bering Sea	63°40′04″N, 170°34′08″W	1950-08	*Cepphus columba*
1738	Eric P. Hoberg	Francis H. Fay	RLR 17687	Saint Lawrence Island, Boxer Bay, Bering Sea	63°20′21″N, 171°34′25″W	1956-08-05	*Cepphus grylle* (Linnaeus, 1758)
27927	Eric P. Hoberg	Eric P. Hoberg	EPH 1303	Saint Matthew Island, Bering Sea	60°20′N, 171°00′W	1982-07-27	*Cepphus columba*
27919	Eric P. Hoberg	Eric P. Hoberg	EPH 1377	Saint Matthew Island, Bering Sea	60°20′N, 171°00′W	1982-07-03	*Cepphus columba*
5732	Eric P. Hoberg	Robert L. Rausch	RLR 13473	Shuyak Island, Big Bay, Gulf of Alaska	58°33′23″N, 152°36′14″W	1954-09-08	*Uria aalge* (Pontoppidan, 1763)
27879	Eric P. Hoberg	Robert L. Rausch	RLR 37301, EPH 572	Sledge Island, Bering Sea	64°29′45″N, 166°12′08″W	1969-07-06	*Cepphus columba*
27928	Eric P. Hoberg	Eric P. Hoberg and Duff H. S. Wehle	EPH 126	Ugaiushak Island, Gulf of Alaska	56°47′N, 156°41′W	1976-07-05	*Cepphus columba*
26828	Eric P. Hoberg	Patrick J. Gearin	EPH 1142	Western Aleutian Islands (pelagic habitat)	ca. 50–51°N, 172–174°E	1981-06-28	*Cerorhinca monocerata* (Pallas, 1811)

Note:

Native software versions of all tables and supplementary tables are attached to the main record for this article.